SYSTEMATICS OF AFRICAN MOLOSSID BATS OF THE SUBGENUS XIPHONYCTERIS OF THE GENUS TADARIDA (MOLOSSIDAE : CHIROPTERA)

by

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A thesis submitted in conformity with the requirements for the Degree of Doctor of Philosophy in the University of Toronto.

Dedicated to the memory of my first teacher,
Ustaz Abd Al-Hadi Abd Al-Gabar, who taught
me to read and write.

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ABSTRACT

The morphological variations of the taxa of African molossid bats (genus Tadarida Rafinesque, 1814) included by Koopman (1975) in his proposed subgenus Xiphonycteris were analysed and compared with five representative taxa of the subgenus Mops.

Sexual dimorphism, geographic variation and phenetic similarities were assessed using 31 morphometric characters of 586 specimens utilizing univariate and multivariate analyses. Eight of the taxa tested for sexual dimorphism showed a clear statistical separation of the sexes, with Tadarida spurrelli being the most dimorphic (in more than 80 per cent of the characters measured) and T. midas the least dimorphic (in 45 per cent of the characters). Accordingly, males and females were analysed separately.

Phenetic similarities were assessed by cluster analysis using correlation coefficients, average taxonomic distance, subsets and minimum spanning trees together with principal component analysis and nonmetric multidimensional scaling.

Geographic variation in female T.(X.) nanula, male and female T. (X.) leonis, male and female T.(X.) thersites and female T. (X.) spurrelli was examined by generalized discriminant function analysis. Morphologic similarities among geographic samples, as indicated by the minimum spanning trees computed from the matrices of the square root of the Mahalanobis' generalized distances and superimposed on

the discriminant configurations, were compared with geographic distances.

Character variations in geographic samples were tested by univariate analysis using Gabriels' sum of the square simultaneous test procedure (SS-STP) and Power's ranked means. Although character variations are clinal in T.(X.) leonis, they are mostly erratic and do not show a clear clinal trend in other taxa. Taxa known as T.(X.) calabarensis, T.(X.) ochraceus and T.(X.) occipitalis are shown to be synonyms of T.(X.) nanula, T.(X.) leonis and T.(X.) thersites respectively. Specimens of a previously undescribed taxon were compared with other taxa, diagnosed and named as a new species.

The five taxa found to be valid in the subgenus Xiphonycteris (T. spurrelli, T. nanula, T. leonis, T. thersites and the new species) were compared phenetically with representative taxa in the subgenus Mops (T. demonstrator, T. condylura, T. trevori, T. congica and T. midas). Results of cluster analysis, principal component analysis and non-metric multidimensional scaling showed that members in both subgenera are phenetically similar.

From a comparison of morphological characters and original descriptions of T. thersites (Thomas, 1903), T. leonis (Thomas, 1908) and T. brachyptera (Peters, 1852), it is shown that T. brachyptera is the earliest available name that includes T. leonis as a synonym. As the holotype

of T. brachyptera has been lost and no lectotype or syntype exists, a neotype is designated and described according to article 75 of the International Commission of Zoological Nomenclature, 1964.

Based on number of lower incisors, the reduction of the last upper molar and the palatal emargination, characters on which the genus Xiphonycteris and later the subgenus were established, Xiphonycteris is shown to be invalid as a genus or as a subgenus. Accordingly, species previously included in the subgenus Xiphonycteris are reassigned to the subgenus Mops.

RÉSUMÉ

Les variations morphologiques des taxa des chauve-souris molossides de l'Afrique (genre Tadarida Rafinesque, 1814) comprises par Koopman (1975) dans le sous-genre Xiphonycteris, proposé par lui, sont analysées et comparées avec cinq taxa typiques du sous-genre Mops.

Le dimorphisme sexuel, la variation géographique et les similitudes phénétiques sont évaluées suivant 31 caractères morphométriques de 586 spécimens, en utilisant des analyses autant univariées que multivariées. Parmis les taxa mis à l'épreuve concernant leur dimorphisme sexuel, huit font clairement preuve d'une distinction entre les sexes, dont Tadarida spurrelli paraît être le plus dimorphique (dans 80% cahactères mesurées) et T. midas le moins dimorphique (dans 45% des caractèrs). C'est pourquoi les mâles et femelles sont séparément analysés.

Les similitudes phénétiques sont évaluées au moyen d'analyse par groupes en utilisant les coéfficient corrélatifs, les distances taxonomiques moyennes, les sous-groupes et les arbres d'embranchement minimal, ainsi que l'analyse des composantes principales et la graduation multidimensionnelle non-mesurée.

La variation géographique de la femelle de la T.(X.) nanula, du mâle et de la femelle de la T.(X.) leonis, du mâle et de la femelle T.(X.) thersites et de la femelle T.(X.) spurrelli est examinée par analyse des fonctions

discriminantes généralisées. Les similitudes morphologiques entre les échantillons géographiques impliquées par les arbres d'embranchement minimal calculées à partir des matrices de la recine carée des distances généralisées selon Mahalanobis, surimposées sur les configurations discriminantes, sont comparées avec les distances géographiques.

ca Les variations des caractères des échantillons géographiques sont mises à l'épreuve au moyen d'analyse univariée, en utilisant le procédé de tests simultanés de la somme des carres, selon Gabriel (SS-STP) et des moyennes classées de Power. Quoique les variations des caractèrs soient déclives chez la T.(X.) leonis, elles sont pour la plupart erratiques et ne montrent pas une tendance déclive nette pour les autres taxa. Les taxa connus sous les noms de T.(X.) calabarensis, T.(X.) ochraceus et T.(X.) occipitalis s'avèrent être des synonymes de T.(X.) nanula, T.(X.) leonis et T.(X.) thersites à leur tour. Un taxon, non décrit jusqu'ici est comparé avec d'autres taxa, diagnostiqué et désigné comme nouvelle espèce.

Les cinq taxa démontrés être valables dans le sous-genre Xiphonycteris (spurrelli, nanula, leonis, thersites et la nouvelle espèce) sont soumis à une comparison phénétique avec les taxa représentatifs du sous-genre Mops (domonstrater, condylura, trevori, congica et midas). Les résultats de l'analyse en groupe, de l'analyse des composantes principales et la graduation multidimensionnelle non-mesurée démontrent que les membre des deux sous phénétiquement semblables.

La comparaison des caractèrs morphologiques et descriptions originales de la T. thersites (Thomas, 1903), la T. leonis (Thomas, 1908) et la T. brachyptera (Peters, 1852), démontre que le nom T. brachyptera est le nom le plus ancien disponible, et que ce nom comprend la T. leonis comme son synonyme. Alors que l'holotype T. brachyptera est perdue et qu'apparemment aucun lectotype, ni syntype n'est pas en existence, un néotype est désigné et décrit, d'après l'art. 75 du Comite International de la Nomenclature Zoologique de 1964.

D'après le nombre des incisives inférieures, la réduction de la dernièr molaire supérieure et l'emargination palatine, caractères a la base desquels le genre Xiphonycteris et, plus tard, le sous-genre ont été etablis-il est maintenant prouvé que la désignation Xiphonycteris n'est pas valide, ni comme genre, ni comme sous-genre. Par conséquent, l'espèces auparavant comprises dans le sous-genre Xiphonycteris sont maintenant assignées de nouveau au sous-genre Mops.

INTRODUCTION

Xiphonycteris spurrelli is a small species of African bats in the family Molossidae of the mammalian order Chiroptera. Dollman (1911) described the genus and species on the basis of two males from Bibianaha, 100 km. west of Kumasi, Ghana, that were collected by Dr. H. G. Spurrell. The type (BMNH 11.1.11.1.) and topotype are deposited in the British Museum (Natural History).

Dollman (1911) erected the new genus Xiphonycteris to include the single species spurrelli after comparing the two specimens with similar taxa in the family Molossidae and found them to differ by having a dental formula of:

$$i.\ \frac{1-1}{1-1},\ c.\ \frac{1-1}{1-1},\ p.\ \frac{2-2}{2-2},\ m.\ \frac{3-3}{3-3} = 28$$

The lower canines have huge cingula that form a bridge over the lower incisors, a single pair of minute teeth.

Beside the two males there is a female in the British Museum (Natural History) (BMNH 53,556) from Achimota, Ghana. Although Rosevear (1965) doubted its assignment to X. spurrelli, De Vree (1969) and Hayman and Hill (1971) confirmed the taxonomic status of the specimen. No further specimens of X. spurrelli were known until a single skin without skull reported by J. A. Allen (1917) from Luluabourg, Kasai Province, Zaire, was later tentatively assigned to X. spurrelli by Koopman (1965).

Although the features considered diagnostic by Dollman in separating X. spurrelli from similar species in the subgenus Mops were not convincing, lack of specimens made resolution of the systematic status of this species difficult.

Basilio (1962) reported a specimen from Fernando Po, Equatorial Guinea. Eisentraut (1964) and Hayman and Hill (1971) mentioned that the Basilio specimen was sent to the American Museum of Natural History for identification, where it was identified as X. spurrelli. A further record was added by Kock (1969) who described a skull of a female in the Senckenberg Natur Museum, Frankfurt (SMF 22023) from Fernando Po, Equatorial Guinea.

The first complete description of females of this species was made by De Vree (1969) who described two (V1324 and V1454) from Adina, Togo. De Vree showed that although the two females resemble the female from Achimota, Ghana, one female (V1454) possessed a minute, second lower incisor on the left side crowded between the left inner incisor and the cingulum of the canine. De Vree (1969) mentioned that there was no space to accommodate a second incisor on the right side. This tooth arrangement contrasts with that of the female (SMF 22023) described by Kock (1969). Kock recorded the presence of what he called a 'supernumerary' lower incisor. This specimen (SMF 22023) has a third lower incisor pushed to the right side posterior to

the first pair of incisors. Accordingly, the number of incisors, which Dollman (1911) considered to be the main diagnostic feature upon which the genus was established appears to be variable.

De Vree (1969) also described two males (V1453 and V1381) from the same locality, Adina, Togo. Jones (1970) contributed to the existing knowledge by describing two males as X. spurrelli from Rio Muni, Equatorial Guinea. Additional collections in the Royal Ontario Museum (ROM) enabled Turner (1970) to study sexual dimorphism in a collection of six males and 16 females from Cameroun.

The genus Xiphonycteris was regarded as monotypic until Koopman (1975) reviewed the bats of the Sudan. In his revision of the taxa in the subgenus Mops, Koopman (1975), citing R. L. Peterson (pers. comm.) pointed out the similarity of X. spurrelli and Tadarida (Mops) nanula and confirmed his conclusions by comparing a male paratype of T. nanula with the male holotype of X. spurrelli. Accordingly he regarded Xiphonycteris to be a subgenus of Tadarida and to include species with open palates and reduced third commissure on M^3 which were formerly grouped in the subgenus Mops, (T. leonis, T. nanula, T. thersites and the poorly-known East African taxon brachyptera). Koopman's justification for suppression of the genus Xiphonycteris to subgeneric rank was to group taxa characterized by a reduced last upper molar and a well-developed

anterior palatal emargination. At the same time he restricted the subgenus Mops to taxa with a reduced last upper molar and a closed anterior palate.

Members of the subgenus Xiphonycteris thus conceived are characterized by having short legs; long spoon-shaped bristles on the outer sides of the feet; ears folded and crested, joined together above the head; dental formula of 28-30; forearm lengths from 26-40 mm; and total lengths of skuls from 14.00--21.50 mm.

The systematic status of members of Xiphonycteris have long remained unclear. In 1917, J. A. Allen described a taxon from a collection made by Herbert Lang and James P. Chapin from Zaire. Allen (1917) considered the colour of the ventral pelage of this bat to be distinctive enough to warrant its recognition as a new species, T. ochraceus. Koopman (1965) had reservations about the validity of T. ochraceus as a species and considered it to be a subspecies of T. leonis (Thomas, 1908) in view of the distance of the type locality of T. ochraceus from that of T. leonis (Sierra Leone). However, Rosevear (1965) and Hayman and Hill (1971) considered T. ochraceus to be a synonym of T. leonis.

Allen also described another species T. occipitalis that was later reviewed by Koopman (1965) and reduced to a subspecies of T. thersites (Thomas, 1908). But Rosevear (1965) failing to detect any differences between T. occipitalis

and T. thersites, considered T. occipitalis to be a synonym of T. thersites.

Another taxon described by Hayman (1940) from Nigeria as a distinct species, T. calabarensis, was later considered by Rosevear (1965) to be a synonym of T. nanula (J. A. Allen, 1917). A summary of different classifications proposed by Rosevear (1965), Hayman and Hill (1971) and Koopman (1975) for taxa in the subgenus Mops and Xiphonycteris is given in Figure 1 (see Robins and Schnell, 1971).

On the other hand, the East African species T. brachyptera which was described by Peters (1852) from Mozambique, remained poorly known because of lack of material from the type locality. Moreover, the holotype originally housed in Berlin Museum has been lost. The only authentic record of anyone having seen the holotype was Dobson (1876, 1878), who recorded an adult female from Sierra Leone as T. brachyptera after comparing it with the holotype. However, Thomas (1908) assigned this specimen to a new species, T. leonis. Although the holotype was excellently described and meticulously drawn, no definitive decision has been made as to what taxon T. brachyptera corresponds with. The description given by Peters might apply either to T. thersites or T. leonis, but in either case the name brachyptera antedates both. If it is proved that T. brachyptera is an early name for either T. thersites or T. leonis, one or the other would become a synonym. However, Rosevear (1965) and Hayman and Hill (1971)

suggested that T. thersites and T. leonis may be colour variants of a single species.

Uncertainties relating to the systematic status of these small African bats have resulted in misidentification of specimens. For example, the specimen (AMNH 233868) that was recorded as T. brachyptera by De Beaux (1922) and Freeman (1977) is actually T. thersites (Fig. 2).

Objectives

In view of the existing confusion regarding the systematic status of the bats in the subgenus Xiphonycteris, this study was conceived to accomplish the following objectives:

1. To use appropriate statistical procedures to investigate phenetic relationships among taxa grouped by Koopman (1975) in the subgenus Xiphonycteris and to examine geographic and sexual variation within these taxa.
2. To clarify the systematic status of species and subspecies of the subgenus Xiphonycteris.
3. To compare valid species and subspecies of the subgenus Xiphonycteris with representative taxa in the subgenus Mops to determine the validity of the two subgenera.
4. To analyse the systematic status and position of a group of specimens discovered by Dr. R. L. Peterson and set aside as a possible undescribed taxon similar in size to T. nanula and T. spurrelli but thought to

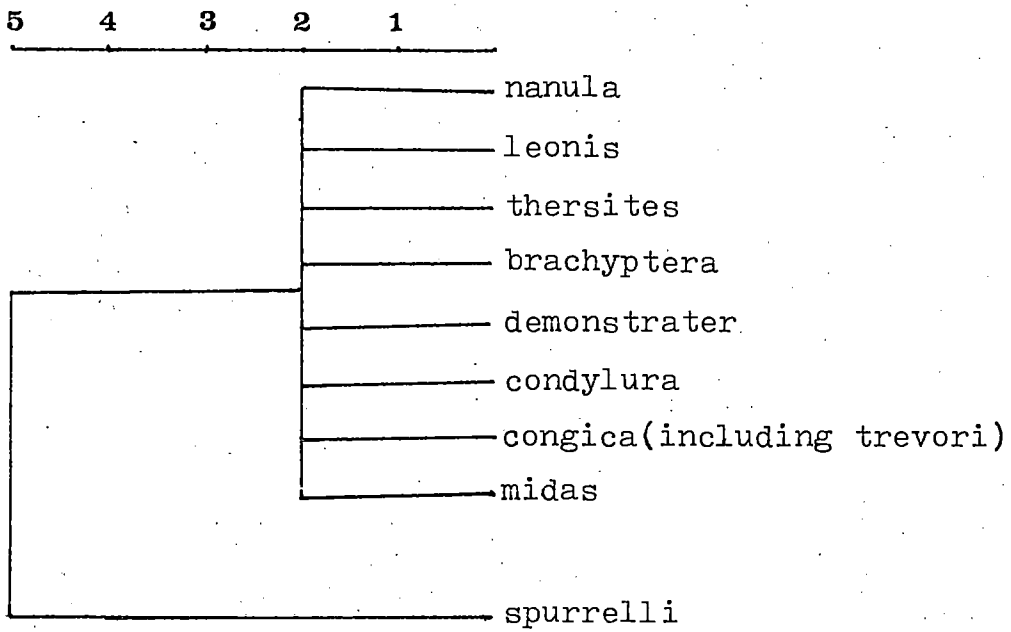
be allied with *T. leonis* and tentatively treated by Peterson as *T.* "subleonis".

5. To diagnose clearly the valid taxa and to provide keys for identification.

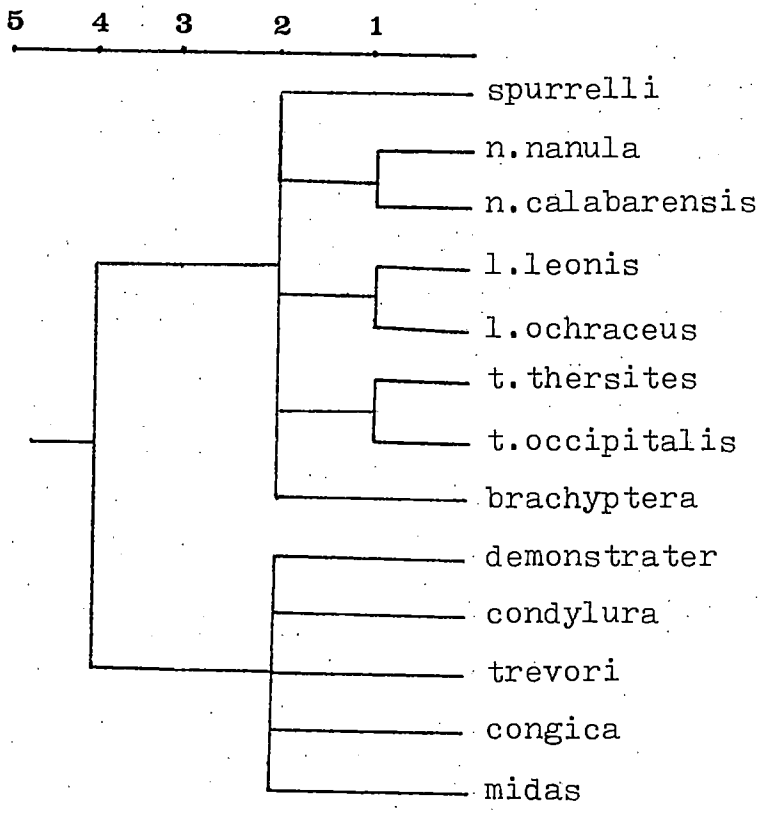
Fig. 1

Dendrograms depicting classifications proposed by Rosevear (1965) and Hayman and Hill (1971), and Koopman (1975). Junctions between stems indicate taxonomic levels. The following arbitrary similarity coefficients were assigned to formal taxonomic levels: (1) subspecies (2) species (3) subgenus (4) genus and (5) family.

Fig. 1



Rosevear(1965) and
Hayman and Hill(1971).



Koopman(1975).

Fig. 2

Dorsal view (A) and ventral view (A*) of T. thersites (AMNH 233868) incorrectly identified as T. brachyptera; compared to T. thersites (USNM 450001),(B) dorsal view (B*) ventral view.

Fig. 2

A B

* *
B A

MATERIALS AND METHODS

Most specimens studied were prepared study skins and skulls. A few were preserved in alcohol with skulls removed. When only skulls or skins were available, they were used exclusively in statistical procedures not requiring complete data sets. Specimens in collections of the following institutions were either made available through loans to Dr. R. L. Peterson or examined personally:

AMNH American Museum of Natural History

BMNH British Musuem (Natural History)

CUMZ Carleton University Museum, Ottawa

CM Carnegie Museum, Pittsburg

LACM Los Angeles County Museum

MCZ Museum of Comparative Zoology, Harvard University

ROM Royal Ontario Museum

SMF Senckenberg Natur Museum, Frankfurt

USNM United States National Museum of Natural History

Characters

Thirty-one morphometric characters were used. Measurements for length of the body, tail, ear, tragus, hindfoot and wingspan are usually taken by collectors using different methods and were not included in analyses. Instead, I used only characters that I measured or similar characters of holotypes measured by Dr. R. L. Peterson.

Characters were measured with Helios dial calipers to the nearest 0.1 mm for wing bones and to the nearest 0.05 mm for cranial measurements. The width of the septum separating the basisphenoid pits (WSBP) and the length of one of the basisphenoid pits (LBSP) were measured under a binocular microscope fitted with an ocular micrometer. Only adult specimens were studied and were characterized by the complete fusion of the epiphysis of matacarpals and phalanges and by the complete fusion of the basisphenoid-basioccipital sutures.

In selecting and describing the following 31 characters, I followed Peterson (1972), Eger (1977), Freeman (1977) and Swanepoel and Genoways (1978):

Wing Measurements (Fig. 3)

1. Forearm (FOAR), length from the olecranon process of the ulna to the shallow notch proximal to the thumb, including carpals.
2. Third metacrapal (3MET), length from the distal end-point of the wrist, including carpals, to the metacarpal--phalangeal joint.
3. First phalanx of the third metacarpal (3M1P), length from the matacarpal-phalangeal joint to the distal end of the first phalanx.
4. Second phalanx of the third metacarpal (3M2P), length from the proximal to the distal end of the second phalanx.

5. Fourth metacarpal (4MET), length from the distal end-point of the wrist, including carpals, to the metacarpal--phalangeal joint.
6. First phalanx of the fourth metacarpal (4M1P), length from the metacarpal-phalangeal joint to the distal end of the first phalanx.
7. Second phalanx of the fourth metacarpal (4M2P), length from the proximal to the distal end of the second phalanx.
8. Fifth metacarpal (5MET), length from the distal end-point of the wrist including carpals, to the metacarpal--phalangeal joint.
9. First phalanx of the fifth metacarpal (5M1P), length from the metacarpal-phalangeal joint to the distal end of the first phalanx.
10. Second phalanx of the fifth metacarpal (5M2P), length from the proximal to the distal end of the second phalanx.

Skull Measurements (Fig. 4)

11. Greatest length of the skull (GSLN), greatest distance from the posterior portion of the occipital bone to the anteriormost projection of the incisors.
12. Condyloincisive length (CDIN), greatest distance from the posteriormost projection of the occipital condyles to the anteriormost projection of the incisors.

13. Palatal length (PALL), greatest distance from the posterior border of the hard palate to the anteriormost edge of the first incisor, excluding any central notch or projection.
14. Zygomatic breadth (ZYGO), greatest width across zygomatic arches measured on the squamosal bone.
15. Mastoid breadth (MAST), greatest width across mastoid processes.
16. Breadth of the braincase (BBCS), greatest width of the braincase above mastoid processes.
17. Height of the braincase (HBCS), distance from basisphenoid and occipital bones to the parietal, not including the sagittal crest.
18. Rostral length (ROWL), distance from the anterior end of the cribriform plate to the anterior borders of the incisors.
19. Interorbital width (IOWA), distance across the rostrum posterior to the lachrymal processes.
20. Postorbital constriction (POCN), distance measured across the least constriction.
21. Width at the upper molars (M3M3), greatest buccal distance between the last upper molars including the alveolar borders.
22. Maxillary toothrow (CANM), distance from the anterior borders of the upper canines to the posterior borders of the last upper molars.

23. Canine to canine width (CANC), distance across the upper canines including the cingula.
24. Canine height (CANH), the height of the canine including the cingulum.
25. Width of the septum between the basisphenoid pits (WBPS), greatest width of the septum separating the basisphenoid pits.
26. Length of the basisphenoid pits (LBSP), the greatest length of one of the basisphenoid pits.

Mandible (Fig. 4)

27. Mandibular condyloincisive length (CNIL), distance from the mandibular condyles to the anterior face of the incisors.
28. Greatest length of the mandible (GMLN), distance from the anterior face of the incisors to the most posterior projection of the angular process.
29. Mandibular toothrow (LCAM), distance from the anterior face of the incisors to the posterior part of the last molar.
30. Width between canines (LCAC), outermost distance between the canines including the cingula.
31. Canine height (LCAH), greatest length of the canine including the cingulum.

Fig. 3

Wing measurements as exemplified by Tadarida (Xiphonycteris) spurrelli (not drawn to scale). Numbers correspond to descriptions given in Materials and Methods.

Fig. 3

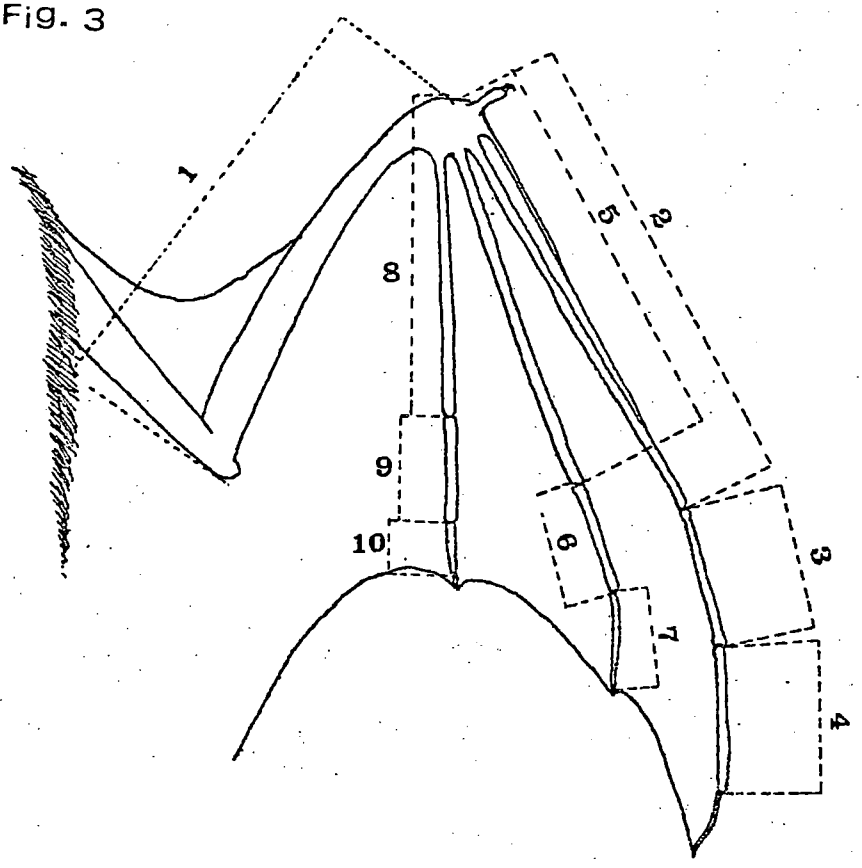
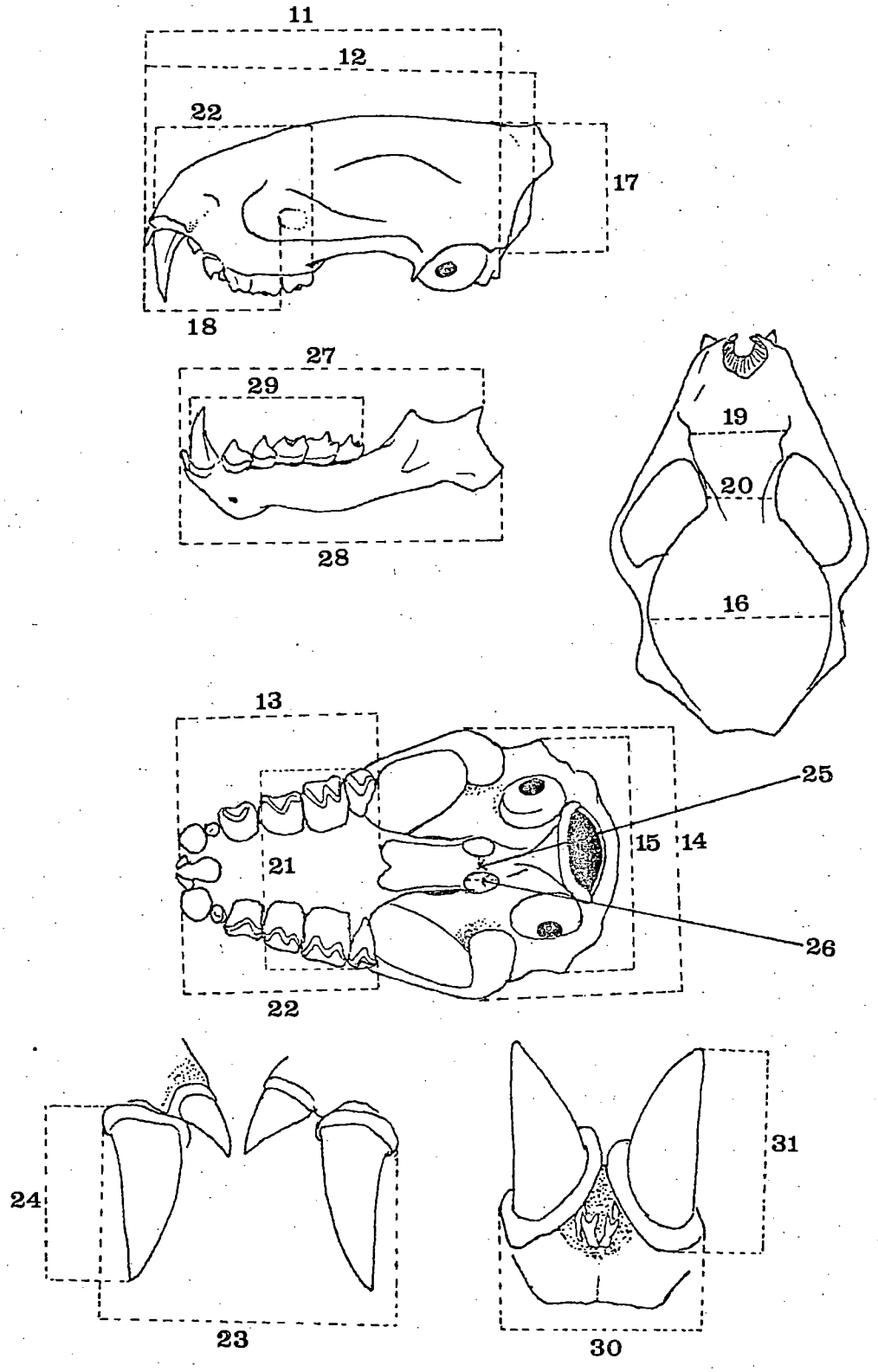


Fig. 4

Measurements taken on skull, mandible, upper and lower incisors as exemplified by T.(X.) spurrelli (not drawn to scale). Numbers correspond to descriptions given in Materials and Methods.

Fig. 4



OTU's

Without the bias of *a priori* groupings, the following taxa were considered Operational Taxonomic Units (OTU's) (Sneath and Sokal, 1973) and referred to in analyses by the abbreviations shown below:

1.	*Tadarida* (*Xiphonycteris*) *spurrelli* (Dollman, 1911)	SPUR
2.	*T.*(*X.*) *nanula* (J. A. Allen, 1917)	NANU
3.	*T.*(*X.*) *calabarensis* (Hayman, 1940)	CALB
4.	*T.*(*X.*) *leonis* (Thomas, 1908)	LEON
5.	*T.*(*X.*) *thersites* (Thomas, 1903)	THER
6.	*T.*(*X.*) *brachyptera* (Peters, 1852)	BRAC
7.	*T.*(*X.*) *ochraceus* (J. A. Allen, 1917)	OCHR
8.	*T.*(*X.*) *occipitalis* (J. A. Allen 1917)	OCCP
9.	A taxon tentatively referred to as *T.* "subleonis"	SBLN
10.	*T.*(*Mops*) *trevori* (J. A. Allen, 1917)	TREV
11.	*T.*(*M.*) *condylura* (Smith, 1833)	COND
12.	*T.*(*M.*) *congica* (J. A. Allen, 1917)	CONG
13.	*T.*(*M.*) *demonstrator* (Thomas, 1913)	DEMO
14.	*T.*(*M.*) *midas* (Sundevall, 1843)	MIDA

Localities

Specimens were grouped by localities according to existing political boundaries. Certain taxa represented by small sample sizes from contiguous localities not separated by geographic barriers were combined into discrete localities.

Specimens in this study had been collected from the following localities or regions abbreviated as shown below:

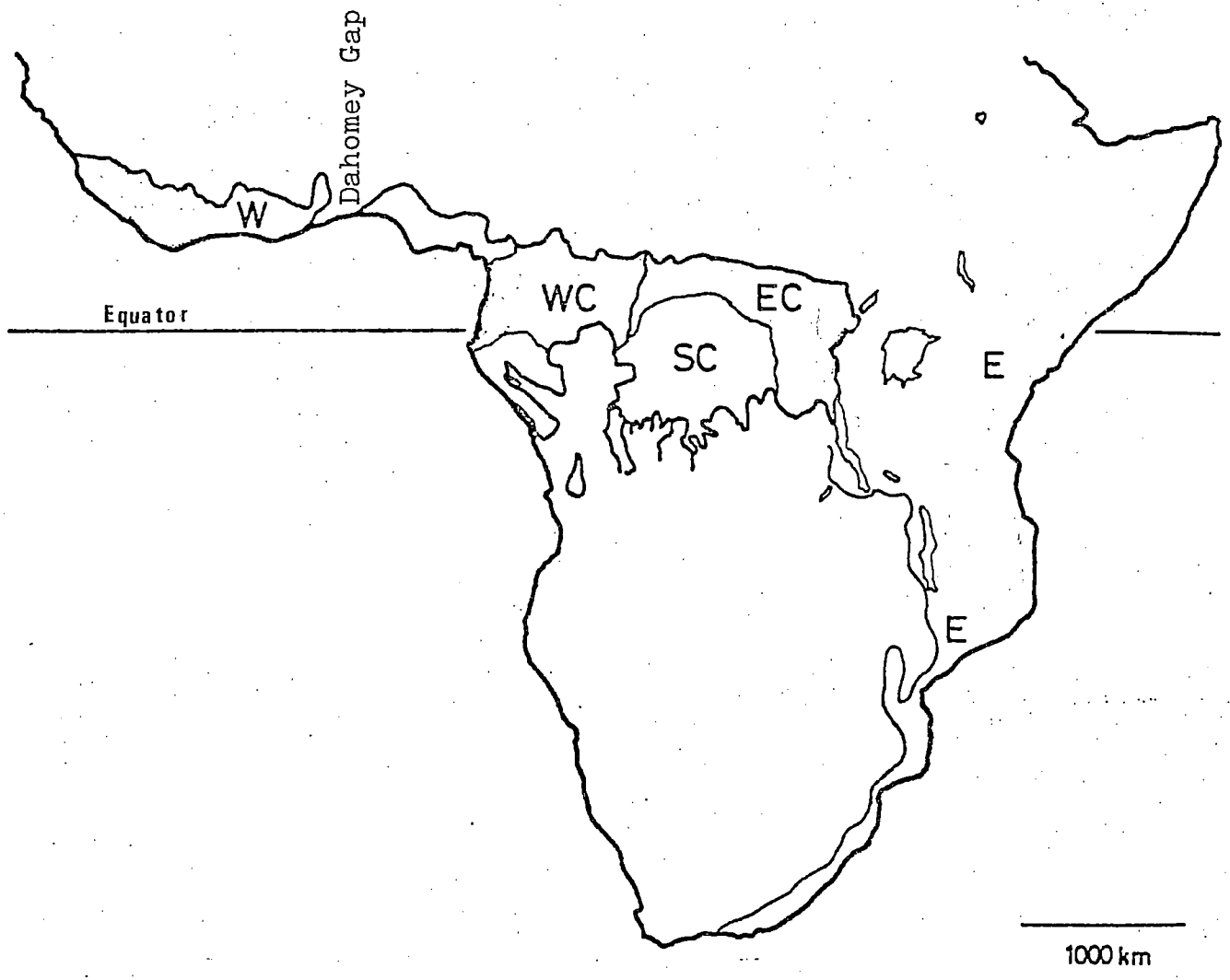
1.	Sierra Leone	SIER
2.	Ivory Coast	IVCO
3.	Ghana	GHAN
4.	Cameroun	CAMR
5.	Central African Republic	CNAF
6.	Sudan	SUDN
7.	Niangara, Zaire	NIAN
8.	Medje, Zaire	MEDJ
9.	Luluabourg, Zaire	LULB
10.	Uganda	UGAN
11.	Kenya	KENA
12.	Rio Muni	RIOM
13.	Botswana	BOTS
14.	Benin (formerly Dahomey)	BENN
15.	Togo	TOGO
16.	Liberia	LIBR
17.	West Africa	WAFR

I followed Grubb (1978) in recognizing major geographic regions and faunistic divisions of the forest biomes in Africa (with slight modifications)(Fig.5). Morphological data were supplemented by such data from specimen tags as longitude, latitude, elevation and dates of collection. Coordinates of localities are recorded from The Times Atlas of the world (1975). Capitalized colour descriptions given here are those of Ridgway (1912).

Fig. 5

Faunistic divisions of the Forest Biome in Africa. W = Western Region; WC = West Central Region; EC = East Central Region; SC = South Central Region; E = Eastern Region (after Grubb, 1978).

Fig. 5



Statistical Procedures

Raw data matrices representing 31 morphometric characters of 586 specimens were subjected to the following statistical analyses using the University of Toronto IBM/ 37-/165 II computer.

Missing Data Estimation

Because of a paucity of material it was necessary to use specimens with missing data. The programme, Missing Data Estimator (MDE), was used to perform a simple linear regression of each variable on every other variable. The variable showing the highest correlation with the variable for which a value was missing was then used to predict the missing value.

Estimating missing data rather than using the means as substitutes for missing variables is preferred by some researchers, e.g., Power and Tamsitt (1973), Gibson et al. (1976) and Eger (1977). Means normally do not retain the general correlation structure among variables as do estimates of missing variables.

Sexual Dimorphism

The sexes were tested for size dimorphism in the following eight OTU's to determine whether they should be treated separately in univariate and multivariate analyses: SPUR, NANU, LEON, THER, SBLN, COND, AND MIDA.

The programme (T-TEST) in the Statistical Package for the Social Sciences (SPSS) written by Nie et al. (1975) was used to assess character differences between the sexes. Because t cannot be computed for the difference in the sample means when samples have unequal variances, an approximation of t was computed. To test for different variances in characters between populations, an F-test of sample variances was performed. When the probability of F was greater than 0.05, a t-value was obtained from the pooled-variance estimate; and when the probability for F was equal to or less than 0.05, a t-value was obtained from the separate variance estimate.

Multivariate analysis of variance (MANOVA) was also used to test over-all character variability between the sexes of each OTU. Pooled within-groups, among groups, total sum of the squares and cross product matrices were computed. A test of significance by the Wilk's likelihood-ratio was performed by calculating the F-value from the determinants of the within matrix and the total matrix (Sokal and Rohlf, 1969). This was followed by two group discriminant analyses (Klecka, 1975) to determine linear functions that maximally separate males and females.

Sample sizes for SBLN, COND, CONG and MIDA were not adequate for MANOVA testing. Instead, only two-group discriminant analysis and t-tests or t-tests alone were used to assess sexual dimorphism in these OTU's.

Within-Group Sample Statistics

Characters means, ranges, standard deviations, standard errors of the means and variances were computed for each sex in each group separately using the programme (UNISTAT) in the Department of Mammalogy of the Royal Ontario Museum. When a taxon was subsequently synonymized with its respective rank, new sample statistics were computed for all members in that rank.

Phenetic Studies

Phenetic affinities among OTU's were assessed by using procedures in the NT-SYS package of multivariate programmes, 1974 version, written by Rohlf et al. (State University of New York at Stony Brook). Phenetic studies involved several procedures, summarized as follows:

Correlation Studies

Two types of correlation studies were carried out: an R-type study which involves correlation among characters and a Q-type analysis which investigates correlations or distances between pairs of OTU's (Cattell, 1952).

R-type Analysis

Raw data were standardized so that each character had a mean of zero and a unit variance. This gave equal weight to all characters and prevented characters with large values

from exerting more influences than those with small values. Product moment correlation coefficients (r) were computed among characters.

Principal Component Analysis

Principal component analysis (PCA) performed on the matrix of correlations between characters is a form of representation of data matrices without a priori assumptions that OTU's fall into a nested series of clusters. Although a certain degree of distortion in the phenetic relationships among similar OTU's does exist, this can be detected by superimposing a minimum spanning tree (MST) on the projected OTU's such that the shortest distances are linked together but no more than N-1 links are generated in the tree, where N is the number of OTU's (Gower and Ross, 1969; Rohlf, 1970). MST is normally computed from the original matrix of dissimilarities between OTU's in such a way that the total length of the lines is at a minimum.

Accordingly, PCA was performed, and the information contained in the original matrix of correlation between characters was summarized in fewer axes or factors, usually three; the first is orthogonal and uncorrelated with the second, whereas the third is orthogonal and uncorrelated with the first and the second. Although the first factor is often considered to be a size factor judging by the high

value of positive or negative loading of characters on it, it can also imply a general description of shape, especially when positive and negative loadings occur on the same factor.

Eigenvalues extracted explain the contribution of each principal component in accounting for the similarity matrix, whereas loadings of characters indicate the relative contribution of each character to the arrangement of the OTU's in the hyperspheroidal space. Coordinates of OTU's were projected onto three-dimensional (3-D) configuration using the programme (PHYSETER), written by Dr. A. R. Gibson at the University of Toronto.

Q-type Analysis

Average linkage cluster analysis using the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal, 1973) was performed on the OTU's correlation matrix resulting in phenograms of correlation coefficents (diagrams of phenetic relationships; Camin and Sokal, 1965). OTU's sharing high positive values are considered to be similar.

Standardized data were also used to generate matrices of average taxonomic distances (d) between OTU's (Sokal, 1961). Results were then summarized in phenograms using UPGMA. OTU's sharing low values are considered to be similar.

Phenograms do not always present an accurate summary of the information contained in the original matrices of similarities and usually distort phenetic relationships especially at lower clustering levels (Sneath and Sokal, 1973) and are accordingly used as broad summaries of relationships (Moss et al., 1977). A measure of goodness of fit was described by Sokal and Rohlf (1962) and Sneath and Sokal (1973) and referred to as the cophenetic correlation coefficient. It is a value computed between coefficients based on the original data matrix and coefficients implied by phenogram and indicates how well a phenogram summarizes its original data matrix. The UPGMA method rather than other clustering procedures was used because it has yielded the highest cophenetic correlation in numerical taxonomic studies (Sokal and Rohlf, 1972; Farris, 1969; Rohlf, 1970). Cophenetic correlation coefficients were computed for all phenograms of similarities.

Multidimensional Scaling

Nonmetric multidimensional scaling (MDSCALE) was described by Kruskal (1964a, 1964b, 1971) and Wish and Carroll (1971). The technique uses the average taxonomic distance, d, as input and moves all coordinates of OTU's by successive iterations so as to decrease stress value (a measure used by Kruskal as goodness of fit between the distances of OTU's i and j in the reduced space of k dimensions and

the original average taxonomic distances). The process is repeated until either the maximum number of iterations or the lowest value of stress is reached.

Results of the MDSCALE were plotted by the programme (PHYSETER) in 3-D diagrams, and MST was superimposed on the resulting configurations. The programme (SUBSETS) was used to locate all subsets (based on the average taxonomic distance) of OTU's satisfying the condition that the greatest dissimilarity between OTU's in the subset is less than the least dissimilarity between any OTU in the subset and any OTU not in the subset.

When results of PCA and MDSCALE were similar, character loadings of PCA were used to interpret the relationship between OTU's in the PCA/MDSCALE 3-D Diagrams (Baker, 1977).

Geographic Variation of Selected Taxa

Geographic variation among populations of the following groups were studied: NANU, LEON, THER and SPUR. Character variation among samples was assessed by univariate analysis of variance using the programme (UNIVAR). Each character was analysed separately, and the variance within and among the samples was computed, followed by F-tests. When results of F-tests were significant (based on 95% confidence limits), Gabriel's sum of the square simultaneous test procedure (SS-STP) was used as an a posteriori method (Gabriel and Sokal, 1969). I used Power's (1970)

modification of SS-STP based on ranked means to establish nonsignificant subsets.

The programme CANAN was used to perform a generalized discriminant functions analysis (Cooley and Lohnes, 1971). The analysis was carried out in steps using multivariate analysis of variance to generate pooled within-groups, among groups, total sums of squares and cross product matrices and a test of significance by the Wilk's likelihood-ratio method.

If significant differences were detected among sample localities, then a generalized discriminant analysis was performed. Factor coefficients produced (scaled vectors times pooled within-group standard deviations) were used to assess the relative contribution of each variable in the maximization of among-group to within-group variations. The procedure adopted followed Seal (1966) in estimating the distance between the mean vectors of each species and reducing the 31 measurements to as few as possible canonical axes that are theoretically uncorrelated with each other.

When only two significant roots were generated, sample localities were projected onto the first two canonical axis with 95% confidence circles drawn around group centroids. When three or more significant roots were produced, sample localities were projected onto the first three canonical axes. The programme PHYSETER was used to plot a 3-D representation of the projections of sample means onto discrimi-

nant axes I, II and III. MST was computed from matrices of the square roots of Mahalanobis' generalized distances ($\sqrt{D^2}$) among samples using the original 31 character space and superimposed on the 3-D diagrams to indicate the possible distortions in the reduced space. MST was also superimposed on maps of geographic locations of samples to demonstrate similarities between geographic and morphologic distances. The programme SUBSETS in NT-SYS based on ($\sqrt{D^2}$) was used to detect the greatest similarities among sample localities. In this procedure I followed Baker et al. (1978).

Raw Data and Results

Raw data and results of this study, such as measurements and computer print outs not given here, are deposited in the Department of Mammalogy of the ROM.

Skull Drawings

Skull drawings were made with a camera lucida in the Department of Vertebrate Paleontology at the ROM. A Wild M5 stereomicroscope at 25X magnification with an M5 Drawing Tube was used to draw the occlusal surface of the third upper molar.

RESULTS

Sexual Dimorphism

SPUR [T.(X.) spurrelli]

Results of t-tests showed that males and females were significantly different in 25 morphological characters, i.e., they differed significantly in more than 80 per cent of the characters measured, with 20 characters showing a probability of less than 0.001. In all 25 characters, males averaged larger than females (Table 1).

Multivariate analysis of variance (MANOVA) showed that character differences between males and females were significant (F transformation of Wilks' Lambda = 43.61; df=31 and 95; $P < 0.001$). When data were subjected to two-group discriminant function analysis, both CANH and LCAC contributed most to the separation of males and females (Table 1). Discriminant scores of individual males and females were plotted along a single discriminant axis resulting in a two-group histogram (Fig. 6). There were no overlaps between the discriminant scores.

NANU [T.(X.) nanula]

Results of t-tests showed that the sexes were significantly different in 21 characters (68 per cent of the characters measured), with 14 characters highly significantly different ($P < 0.001$).

MANOVA showed that males and females differ significantly (F transformation of Wilks' Lambda = 14.29; df=31 and 42; $P < 0.001$). In the two-group discriminant function analysis 4M2P was the most highly loaded character on the discriminant axis (negative loading), although it did not differ significantly in the sexes in the t-test (Table 2). This is due to the fact that in the discriminant analysis character variations and covariations are considered simultaneously among all characters while the t-test only examines variations in one character at a time. The negative sign showed that 4M2P maximally separates males and females towards the negative side of the discriminant axis (Fig. 7). However, only characters that load highly and display significant results in the t-tests are considered in this study to be discriminatory. Accordingly, CANC and CDIN contributed predominantly in the separation of males and females (Table 2). The histogram showed clear separation between the sexes without noticeable overlap. The relatively small sample size of males as compared to females influenced the distribution of the scores of males along the discriminant axis (Fig. 7).

LEON [*T.(X.) leonis*]

The t-test results showed that males and females were significantly different in 21 characters (68% of all the characters measured), with 13 characters showing a probabilty

of less than 0.001. MANOVA showed that males and females differed significantly (F transformation of Wilks' Lambda = 23.12; df=31 and 57; $P < 0.001$). Although WBSP showed a high negative loading in the discriminant analysis, it also showed a non-significant result in the t-tests. Therefore, LCAM and CANC were considered to be best discriminators between the sexes as they load highly and show significant results in the t-tests (Table 3). The histogram showed a clear separation of the sexes along the discriminant axis without any apparent overlap (Fig. 8).

THER [T.(X.) thersites]

Results of t-tests showed that the sexes were significantly different in 21 characters (68% of the total characters measured), with 15 characters showing a probabilty of less than 0.001. MANOVA showed that there was a significant difference between males and females (F transformation of Wilks' Lambda = 16.49; df=31 and 106; $P < 0.001$). In the discriminant analysis LCAH and CNIL contributed predominantly in the separation of the sexes along the positive and the negative sides of the discriminant axis, respectively (Table 4). The histogram showed clear separation of the sexes, but some overlapping is apparant in the histogram (Fig. 9).

SBLN (T. "subleonis")

The sample size was not adequate for a MANOVA test because it requires the number of variables to be less than

the smaple size. Consequently, only a two-group discriminant analysis and a t-test were conducted.

Results of the t-tests showed that males and females were significantly different in 21 characters (68% of all the characters measured), with 11 characters showing a probability of less than 0.001. In all of the 21 characters, males averaged larger than females (Table 5).

In the discriminant analysis GSLN and 5MET contributed to the separation of the sexes (Table 5).

The two-group histogram showed complete separation of males and females without any apparent overlap of the discriminant scores (Fig. 10).

COND [T.(M.) condylura]

Sample sizes for this group were too small for a MANOVA test and for a two-group discriminant analysis. Therefore, only t-tests were performed. The t-tests results showed that males and females were significantly different in 19 characters (61% of the total characters measured), with eight characters showing a probability of less than 0.001. Males averaged larger than females in a all of the 19 characters (Table 6).

CONG [T.(M.) congica]

Because of small sample size, only t-tests were conducted between males and females of this group. Results of

t-tests showed that the sexes are significantly different in 16 characters (52% of all the characters measured), with nine characters showing a probability less than 0.001. Where males and females were significantly different, males averaged larger than females (Table 7).

MIDA [*T.(M.) midas*]

Only *t*-tests were performed because of small sample sizes of males and females. The sexes were significantly different in 14 characters (45% of the characters measured), with four characters showing a probability less than 0.001 (Table 8), and males averaged larger than females in all 14 characters.

Results of the *t*-tests in the species examined are shown as percentages in Fig. 11. *T.(X.) spurrelli*, the smallest of the species, is the most dimorphic (80% of the characters measured), and *T.(M.) midas*, the largest, is the least dimorphic (only 45% of characters).

TABLE 1

Statistical analyses of sexual dimorphism in 54 male and 73 female Tadarida spurrelli.

Characters	Mean		Standardized Discriminant Weights	t-value
	Males	Females		
FOAR	28.33	27.96	-0.0300	2.65**
3MET	29.59	29.04	-0.0472	5.03***
3M1P	10.77	10.53	-0.0308	3.19**
3M2P	10.59	10.30	0.0576	3.37***
4MET	28.46	27.85	0.1959	4.49**
4M1P	8.96	8.83	0.0197	1.43NS
4M2P	6.82	6.73	0.0527	0.82NS
5MET	19.81	19.32	0.1761	4.15***
5M1P	7.19	6.94	0.0063	3.67**
5M2P	2.52	2.44	-0.0263	1.63NS
GSLN	16.04	15.23	0.0239	10.79***
CDIN	14.89	14.06	0.1182	11.77***
PALL	6.67	6.07	-0.0184	11.49***
ZYGO	10.24	9.76	0.2034	8.77***
MAST	9.58	9.18	0.2614	2.39**
BBCS	8.11	7.67	0.1256	3.67***
HBCS	4.87	4.64	0.1069	2.70**
ROWL	5.70	5.20	-0.1858	6.06***
IOWA	4.70	4.30	-0.2480	5.06***
POCN	3.28	3.25	0.2898	1.07NS
M3M3	7.08	6.87	0.2787	6.12***
CANM	6.17	5.70	0.0674	11.77***
CANC	4.70	3.93	0.3231	20.79***
CANH	3.18	2.33	0.6486◀	31.56***
WBSP	0.80	0.79	-0.0939	0.66NS
LBSP	0.82	0.84	0.0088	-1.39NS
CNIL	11.26	10.52	-0.2249	13.49***
GMLN	11.72	11.00	0.0888	11.12***
LCAM	6.89	6.27	-0.1001	15.83***
LCAC	2.39	1.80	0.4364◀	22.15***
LCAH	2.70	1.80	0.3382	14.95***

*** :P < 0.001; ** :P < 0.01; * :P < 0.05; NS : not significant;

◀: characters that maximally separate males and females.

Refer to text for character abbreviations.

Fig. 6

Frequency distribution of discriminant scores for male and female T.(X.) spurrelli along the discriminant axis. Group Centroids are indicated by arrows.

Fig. 6

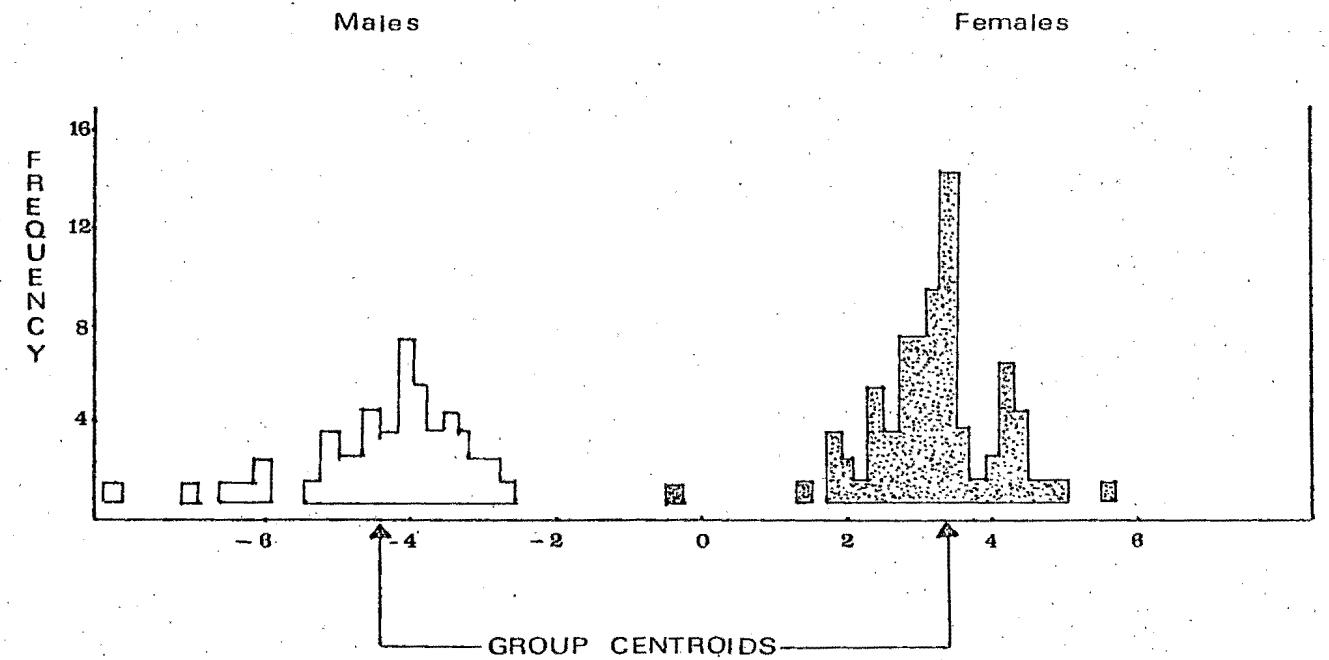


TABLE 2

Statistical analyses of sexual dimorphism in 18 male and 56 female Tadarida nanula

Character	Mean		Standardized Discriminant Weights	t-value
	Males	Females		
FOAR	30.06	28.62	0.1144	1.97*
3MET	30.96	30.49	0.1623	2.31*
3M1P	11.71	11.60	-0.3409	0.75 NS
3M2P	11.38	11.08	-0.3402	2.01*
4MET	30.06	29.33	0.0318	2.73**
4M1P	9.11	9.38	-0.7539	-0.96 NS
4M2P	7.50	7.97	-0.9720	-1.71 NS
5MET	20.29	20.25	0.0218	0.33 NS
5M1P	7.78	7.72	-0.1887	0.45 NS
5M2P	2.94	2.92	-0.3264	0.26 NS
GSLN	16.39	15.75	-0.3397	4.12***
CDIN	15.29	14.61	0.8765◂	6.80***
PALL	6.76	6.36	-0.7338	4.19***
ZYGO	10.42	9.97	-0.1565	4.27***
MAST	9.79	9.58	0.3700	2.65*
BBCS	8.28	8.16	0.2595	1.12 NS
HBCS	4.79	4.75	0.1310	0.67 NS
ROWL	5.93	5.43	-0.3969	6.56***
IOWA	4.54	4.23	-0.0765	2.88**
POCN	3.49	3.41	0.3023	2.06*
M3M3	7.41	7.16	-0.0965	4.70***
CANM	6.11	5.83	0.3074	5.10***
CANC	4.76	4.16	0.9334◂	10.58***
CANH	3.17	2.48	0.6123	12.54***
WBSP	0.97	0.96	0.3455	0.50 NS
LBSP	0.95	0.95	0.0266	0.05 NS
CNIL	11.35	10.79	0.5797	5.98***
GMLN	11.82	11.23	-0.1093	6.42***
LCAM	6.87	6.43	-0.5868	8.09***
LCAC	2.25	1.91	-0.0082	9.30***
LCAH	2.59	1.86	-0.3426	12.84***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.5$; NS: not significant;
◂characters that maximally separate males and females.

Refer to text for character abbreviations.

Fig. 7

Frequency distribution of discriminant scores for male and female T.(X.) nanula along the discriminant axis. Group centroids are indicated by arrows.

Fig.7

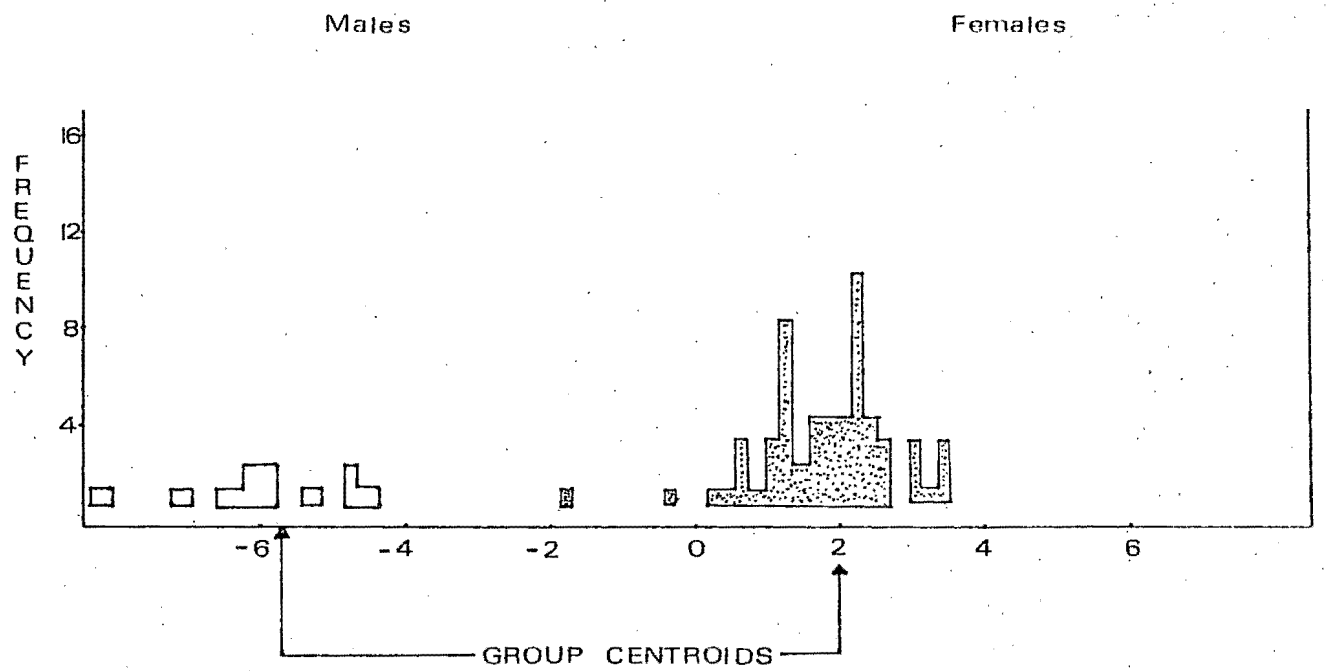


TABLE 3

Statistical analyses of sexual dimorphism in 35 male and 54 female Tadarida leonis

Character	Mean		Standardized Discriminant Weights	t-value
	Males	Females		
FOAR	36.54	36.17	0.2140	1.79 NS
3MET	38.28	37.97	0.0886	1.27 NS
3M1P	14.70	14.38	-0.2060	2.87**
3M2P	14.55	14.12	0.0846	1.75 NS
4MET	36.87	36.60	0.2313	1.11 NS
4M1P	11.86	11.71	0.3347	1.33 NS
4M2P	8.21	8.37	0.2126	-0.97 NS
5MET	24.84	24.46	-0.0196	1.99*
5M1P	9.63	9.56	0.0305	0.52 NS
5M2P	3.28	3.12	-0.1736	2.78**
GSLN	19.08	18.22	0.1915	9.74***
CDIN	17.46	16.67	0.1255	8.21***
PALL	7.64	7.20	-0.5182	8.28***
ZYGO	11.97	11.49	0.3130	5.49***
MAST	10.90	10.64	0.6310	4.49***
BBCS	9.47	9.13	-0.1421	7.40***
HBCS	5.84	5.66	-0.2236	3.42**
ROWL	6.66	6.23	-0.0459	9.46***
IOWA	5.24	5.07	0.0934	3.07**
POCN	3.83	3.79	-0.1087	1.21 NS
M3M3	8.01	7.82	0.6385	3.10**
CANM	6.72	6.41	0.0024	7.69***
CANC	5.27	4.73	-0.7398◂	8.53***
CANH	3.53	2.82	-0.6673	12.91***
WBSP	0.88	0.86	-0.9447	0.61 NS
LBSP	1.31	1.29	-0.1227	1.49 NS
CNIL	12.95	12.15	-0.1584	14.12***
GMLN	13.60	12.92	-0.4940	7.13***
LCAM	7.39	7.11	0.7446◂	2.40*
LCAC	2.60	2.41	-0.6516	2.10*
LCAH	2.77	2.10	-0.7184	20.23***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; NS: not significant

◂characters that maximally separate males and females

Refer to text for character abbreviations.

Fig. 8

Frequency distribution of discriminant scores for male and female T.(X.) leonis along the discriminant axis. Group centroids are indicated by arrows.

Fig.8

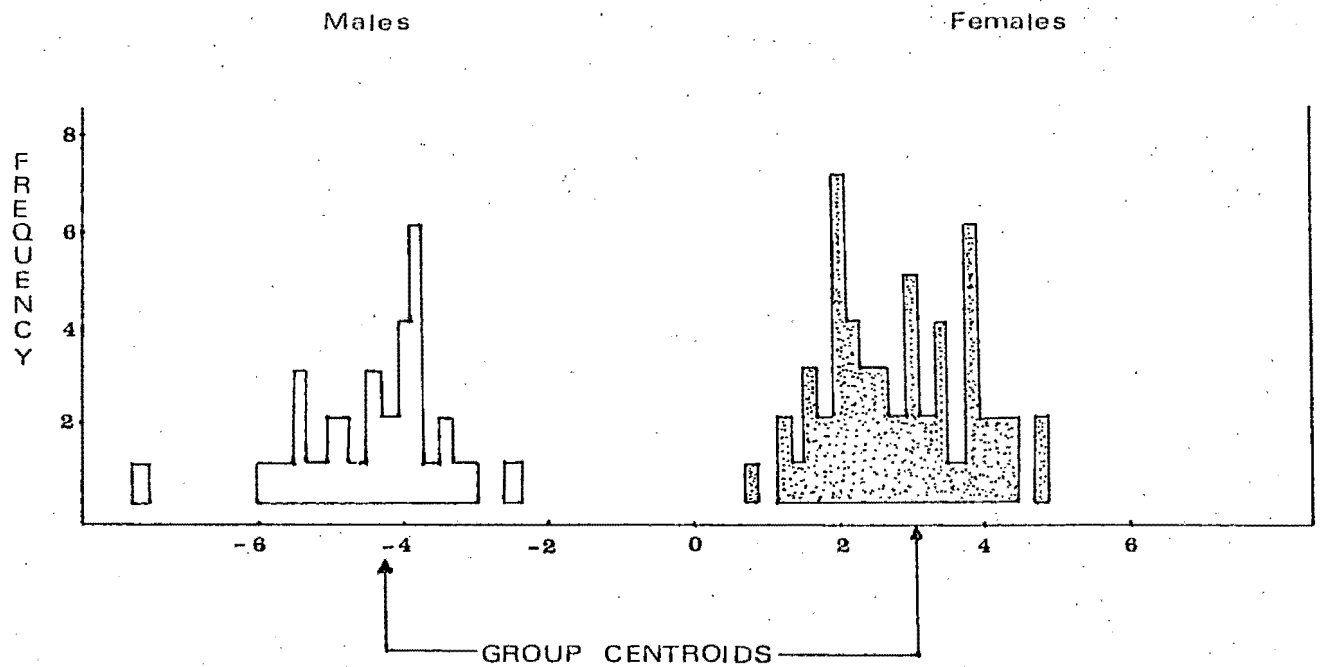


TABLE 4

Statistical analyses of sexual dimorphism in 61 male and 77 female Tadarida thersites

Character	Mean		Standardized Discriminant Weights	t-value
	Males	Females		
FOAR	38.46	38.30	-0.1027	0.67 NS
3MET	40.12	39.92	-0.3324	0.92 NS
3M1P	16.49	16.33	-0.1882	1.64 NS
3M2P	15.78	15.67	0.1152	0.84 NS
4MET	38.56	38.25	-0.1503	1.48 NS
4M1P	13.58	13.41	0.0673	1.66 NS
4M2P	10.94	10.88	0.0558	0.46 NS
5MET	26.30	26.11	0.1222	1.09 NS
5M1P	10.62	10.35	0.0061	3.31**
5M2P	3.40	3.29	-0.1267	2.02*
GSLN	19.39	18.52	0.1097	7.36***
CDIN	17.91	17.16	0.4976	9.10***
PALL	7.84	7.44	-0.0037	7.81***
ZYGO	12.21	11.71	0.0125	7.22***
MAST	11.30	10.98	-0.1155	5.19***
BBCS	9.70	9.53	0.0757	4.01***
HBCS	5.88	5.75	-0.2374	3.23**
ROWL	6.80	6.42	-0.1318	6.85***
IOWA	5.36	5.20	0.0523	3.20**
POCN	3.99	3.94	-0.0305	1.55 NS
M3M3	8.27	8.10	0.1900	3.55**
CANM	6.78	6.58	0.0734	4.76***
CANC	5.46	4.99	-0.0595	10.38***
CANH	3.61	2.88	0.4106	18.14***
WBSP	1.29	1.27	-0.1579	1.25***
LBSP	0.83	0.80	-0.0674	2.02 NS
CNIL	13.38	12.84	-0.6398 ◂	7.76*
GMLN	14.13	13.49	0.4060	9.03***
LCAM	7.55	7.26	0.2623	7.09***
LCAC	2.75	2.44	0.0315	11.87***
LCAH	2.81	2.17	0.8136 ◂	17.70***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.5$; NS: not significant

◂ characters that maximally separate males and females.

Refer to text for character abbreviations.

Fig. 9

Frequency distribution of discriminant scores for male and female T.(X.) thersites along the discriminant axis. Group centroids are indicated by arrows.

Fig.9

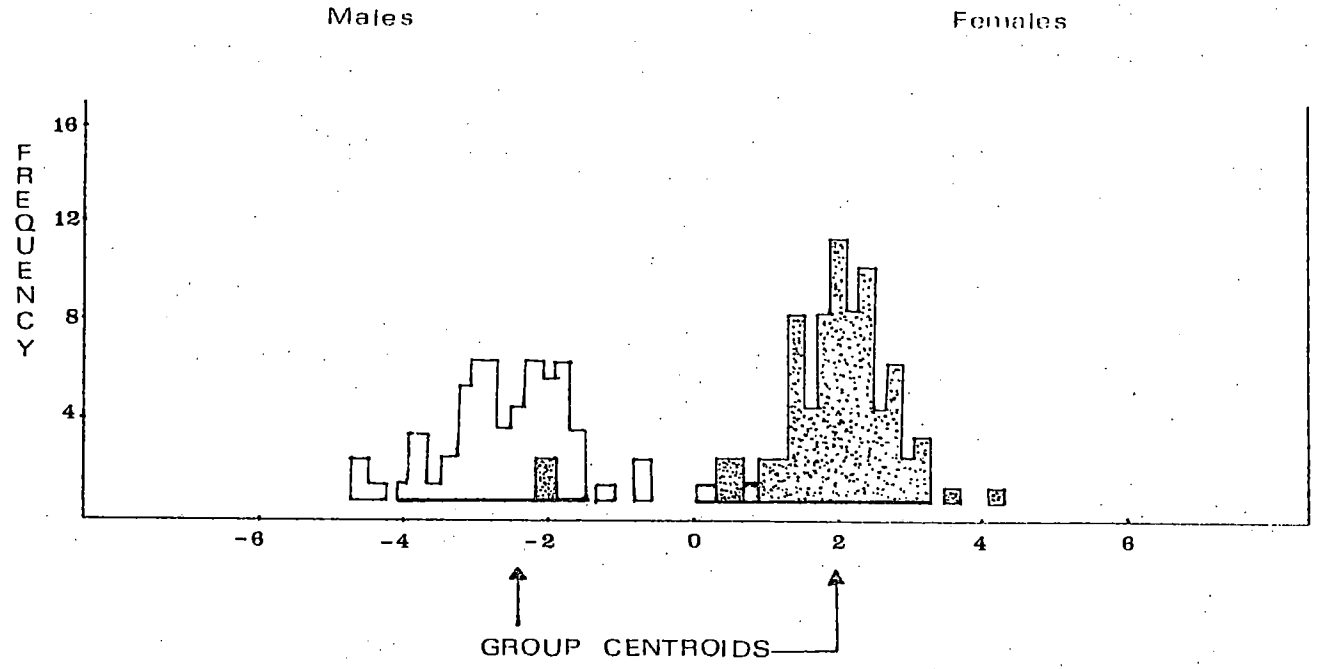


TABLE 5

Statistical analyses of sexual dimorphism in 14 male and 23 female Tadarida "subleonis"

Character	Mean		Standardized Discriminant Weights	t-value
	Males	Females		
FOAR	33.79	33.39	-1.0952	2.02 NS
3MET	35.23	34.85	-3.0024	1.42 NS
3M1P	13.02	12.72	0.7721	2.17*
3M2P	12.55	12.13	0.3565	2.66*
4MET	33.33	33.15	-0.6149	0.41 NS
4M1P	10.74	10.32	0.6984	2.44*
4M2P	8.04	7.10	0.0842	2.51*
5MET	22.59	21.96	-2.3372◂	2.61*
5M1P	9.15	8.78	0.2877	2.46*
5M2P	2.85	2.83	-1.1309	0.23 NS
GSLN	17.08	16.65	2.8379◂	3.51**
CDIN	15.94	15.47	0.4063	3.86***
PALL	6.86	6.56	0.1995	4.37***
ZYGO	10.98	10.52	0.1422	5.85***
MAST	10.22	9.92	0.1360	3.48**
BBCS	8.76	8.59	0.5820	2.69*
HBCS	5.65	5.53	-0.7662	1.75 NS
ROWL	5.76	5.42	0.8558	4.18***
IOWA	4.25	4.12	-0.6410	1.52 NS
POCN	3.46	3.41	-0.0559	1.12 NS
M3M3	7.42	7.29	-0.2842	2.58*
CANM	5.99	5.90	0.5064	1.51 NS
CANC	4.67	4.22	0.8806	7.55***
CANH	3.09	2.47	1.6959	8.46***
WBSP	0.76	0.75	-0.4637	0.08 NS
LBSP	1.18	1.13	0.7112	1.61 NS
CNIL	11.48	11.10	1.7945	4.02***
GMLN	12.23	11.89	1.0901	4.20***
LCAM	6.64	6.42	-0.0143	4.20***
LCAC	2.22	2.04	-0.8397	5.45***
LCAH	2.34	1.91	0.2193	9.63***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; NS: not significant

◂ characters that maximally separate males and females.

Refer to text character abbreviations.

Fig. 10

Frequency distribution of discriminant scores of male and female T."subleonis" along the discriminant axis. Group centroids are indicated by arrows.

Fig. 10

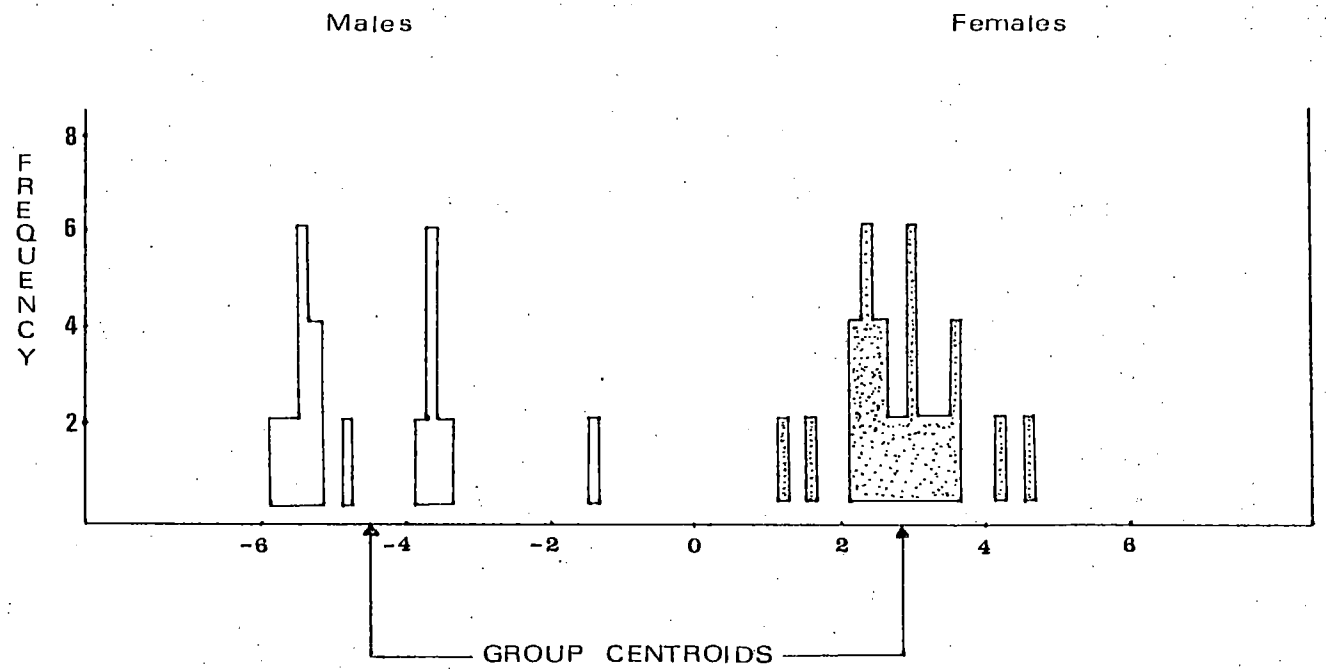


TABLE 6

Statistical analysis of sexual dimorphism in 10 male and 10 female Tadarida condylura

Character	Mean		t-value
	Males	Females	
FOAR	45.92	45.61	0.60 NS
3MET	47.98	46.80	2.79*
3M1P	21.77	20.98	2.66*
3M2P	20.89	20.48	1.10 NS
4MET	46.40	45.43	2.16*
4M1P	17.74	17.37	1.01 NS
4M2P	15.94	15.08	2.13*
5MET	32.02	31.05	2.05 NS
5M1P	12.98	12.74	1.25 NS
5M2P	4.83	4.81	0.14 NS
GSLN	21.42	20.42	5.09***
CDIN	19.20	18.35	4.57***
PALL	8.80	8.36	2.53*
ZYGO	13.17	12.56	4.78***
MAST	11.96	11.68	2.01 NS
BBCS	10.58	10.36	2.27*
HBCS	7.63	6.98	3.04**
ROWL	7.59	7.20	3.06**
IOWA	6.84	6.42	3.03**
POCN	4.49	4.41	1.51 NS
M3M3	9.05	8.80	2.51*
CANM	7.47	7.17	4.21**
CANC	6.23	5.63	9.41***
CANH	4.36	3.54	10.20***
WBSP	1.62	1.60	0.32 NS
LBSP	0.94	0.94	0.11 NS
CNIL	14.57	13.79	5.26***
GMLN	15.09	14.40	5.28***
LCAM	8.36	8.04	-0.50 NS
LCAC	3.04	2.79	-0.50 NS
LCAH	3.41	2.83	7.16***

***: $P < 0.001$; **: $P < 0.01$

*: $P < 0.05$; NS: not significant.

See text for character abbreviations.

TABLE 7

Statistical analysis of sexual dimorphism in 8 male and 12 female *Tadarida congica*

Character	Mean		t-value
	Males	Females	
FOAR	56.91	56.40	0.94 NS
3MET	58.61	57.75	1.52 NS
3M1P	25.73	25.23	0.93 NS
3M2P	22.25	21.66	1.41 NS
4MET	56.25	55.57	1.52 NS
4M1P	21.28	21.12	0.42 NS
4M2P	10.69	10.36	1.01 NS
5MET	33.53	32.88	1.75 NS
5M1P	16.03	15.67	1.39 NS
5M2P	4.93	4.81	0.43 NS
GSLN	25.91	25.25	3.72**
CDIN	23.65	23.04	3.93**
PALL	10.45	9.86	4.89***
XYGO	15.67	15.25	3.48**
MAST	13.90	13.60	1.92 NS
BBCS	12.48	12.18	2.50*
HBCS	8.05	7.84	2.47*
ROWL	9.19	8.65	5.64***
IOWA	7.98	7.57	3.41**
POCN	4.81	4.75	0.77 NS
M3M3	10.74	10.58	1.59 NS
CANM	9.33	9.10	3.40**
CANC	7.63	7.03	5.60***
CANH	5.26	4.61	7.53***
WBSP	0.84	0.83	0.23 NS
LBSP	1.80	1.83	0.20 NS
CNIL	17.97	17.45	4.42***
GMLN	18.81	18.15	4.45***
LCAM	10.56	10.08	5.88***
LCAC	3.66	3.27	6.43***
LCAH	4.26	3.57	7.90***

***: $P < 0.001$; **: $P < 0.01$;

*: $P < 0.05$; NS: not significant.

Refer to text for character abbreviations.

TABLE 8

Statistical analysis of sexual dimorphism in 10 male and 10 female *Tadarida midas*

Character	Mean		t-value
	Males	Females	
FOAR	62.84	62.23	0.84 NS
3MET	63.84	63.77	0.81 NS
3M1P	27.24	26.93	0.78 NS
3M2P	26.63	26.28	0.69 NS
4MET	61.28	61.76	-1.15 NS
4M1P	21.91	21.68	0.66 NS
4M2P	16.40	16.19	0.57 NS
5MET	37.96	37.90	0.15 NS
5M1P	18.45	18.36	0.32 NS
5M2P	7.30	7.27	0.12 NS
GSLN	28.30	27.02	4.79***
CDIN	25.48	24.63	4.87***
PALL	11.39	10.95	4.19**
ZYGO	17.23	16.76	2.40*
MAST	14.83	14.51	2.19*
BBCS	12.69	12.56	0.99 NS
HBCS	8.61	8.37	1.54 NS
ROWL	9.58	9.32	1.77 NS
IOWA	9.42	8.92	3.13**
POCN	4.62	4.55	0.98 NS
M3M3	12.44	12.15	2.35*
CANM	10.57	10.21	3.01**
CANC	8.38	7.72	4.96***
CANH	5.28	4.63	5.89***
WBSP	1.39	1.34	0.58 NS
LBSP	1.98	2.11	-1.34 NS
CNIL	18.70	18.10	3.91**
GMLN	19.45	18.87	4.12**
LCAM	11.79	11.41	3.94**
LCAC	4.23	3.85	-0.89 NS
LCAH	4.70	4.35	3.08**

***: $P < 0.001$: **: $P < 0.01$;

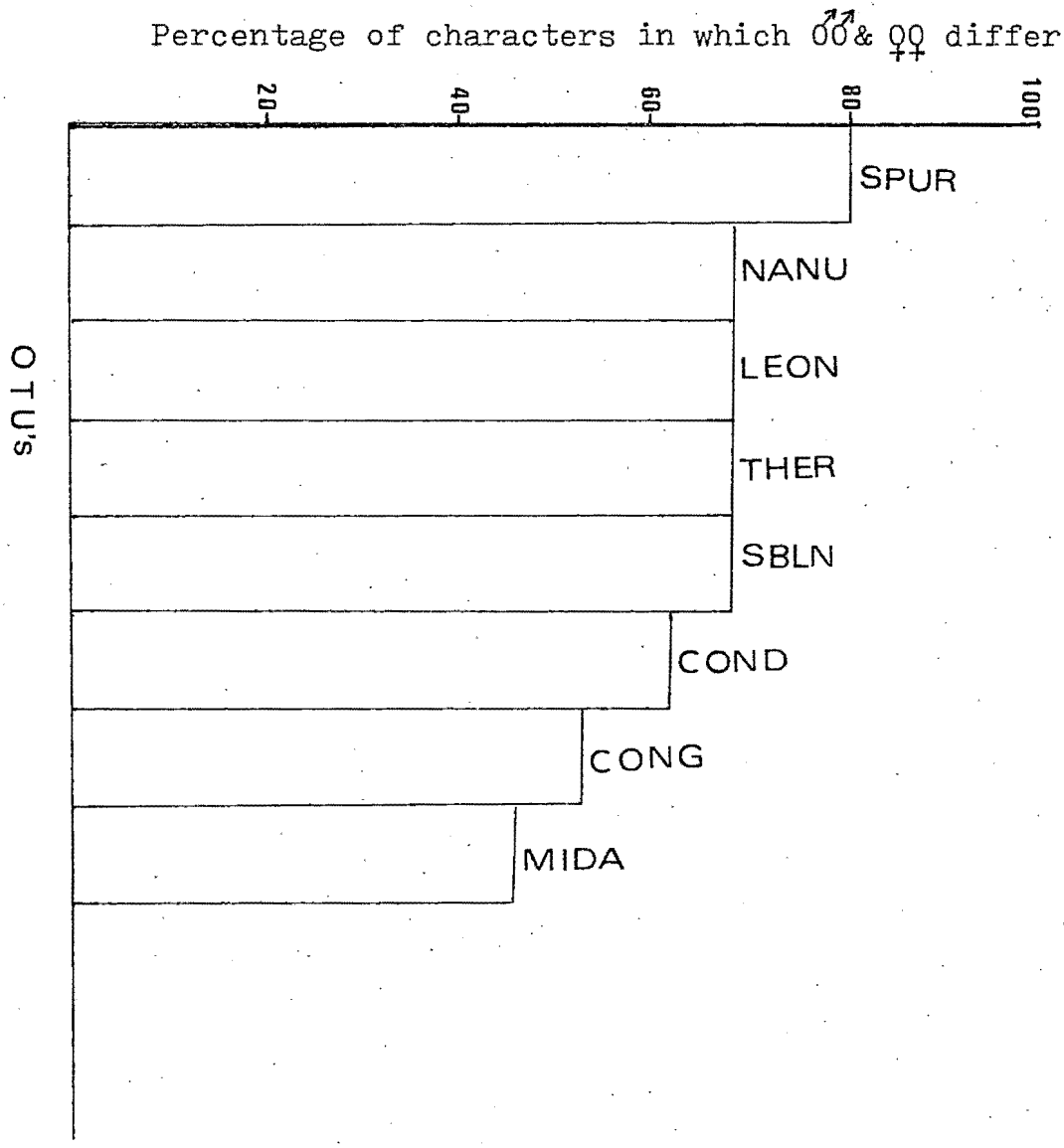
*: $P < 0.05$; NS: not significant.

Refer to text for character abbreviations.

Fig. 11

Percentage of characters in which males and females differ in the species studied. See text for explanation of OTU's abbreviations.

Fig. 11


Percentage of characters in which ♂♂ & ♀♀ differ
20
40
60
80
100
SPUR
NANU
LEON
THER
SBLN
COND
CONG
MIDA
OTU's

Phenetic Similarities

As it has been shown that males and females are sexually dimorphic, they are treated separately in the ensuing study. All taxa grouped under the subgenus Xiphonycteris are recognized here as operational taxonomic units (OTU's).

Cluster Analysis

The phenogram of correlation coefficients for males revealed the existence of three clusters. The first cluster consisted of NANU, CALB and SPUR, and the second of THER and OCCP. The third grouping was of LEON, OCHR, BRAC and SBLN (Fig. 12). The cophenetic correlation coefficient was 0.819.

On the other hand, the phenogram of correlation coefficients for females displayed similar hierarchical groupings. It differed only in joining NANU and SPUR at a higher level and by CALB joining NANU and SPUR at a lower level. In both phenograms THER and OCCP joined the NANU complex, and SBLN joined the LEON complex (Fig. 13).

Average Taxonomic Distance

The phenogram of average taxonomic distance for males differed to some extent from the phenogram of correlation coefficients. Neverthreless, it confirmed the existence of three clusters. The first cluster grouped NANU, CALB, SPUR

and SBLN. The second cluster grouped LEON, BRAC and OCHR. The third cluster grouped THER and OCCP (Fig. 14). The cophenetic correlation coefficient was 0.955.

The phenogram of average taxonomic distance for females presented an identical grouping to that of males, with the exception of BRAC, which joined LEON and OCHR at a lower level (Fig. 15). The cophenetic correlation coefficient was 0.911.

In both phenograms of average taxonomic distance THER and OCCP joined the LEON group instead of NANU group. As taxonomic distances order taxa by size, the presence of THER and OCCP with the LEON group is expected. Although there are no significant differences in size between the THER and LEON groups, THER is nonetheless slightly larger than LEON in wing measurements.

In spite of reservations expressed by Rohlf and Sokal (1965) regarding size-ordered classification from distance matrices, phenograms of the average taxonomic distance are preferable because they have higher cophenetic correlations and thus provide better summaries of the similarity matrices. These phenograms also correspond with results of ordination techniques (see beyond).

Principal Component Analysis/Multidimensional Scaling

Principal component analysis (PCA) based on a matrix of character correlations was used as an initial input for

nonmetric multidimensional scaling (MDSCALE) to minimize the distortion of the close-relative relationships between OTU's that PCA normally causes (Rohlf, 1972; Webster, 1975). However, character loadings on the first three principal components were used to interpret the placement of OTU's along the axes of the MDSCALE configuration. For male OTU's the three principal components accounted for 96.92 per cent of the total character variance among OTU's (86.36% by the first component, 6.16% by the second, and 4.40% by the third).

The loading of characters on the first component was positive and with high values for all characters except LBSP and WBSP, which gave positive loadings but small values and therefore helped to separate the OTU's predominantly on the basis of size (Table 9). The LEON group and SBLN have large basisphenoid pits and are separated from the THER and NANU groups, which have small basisphenoid pits (Fig. 16). The second component separates OTU's on negative loading of LBSP and HBCS and on the positive loadings of WBSP and LCAH. The third component separates OTU's on the basis of the negative loadings of LCAH and LCAM and positive loading of 4M2P. It is appropriate to mention here the intermediate position occupied by SBLN in connecting NANU with LEON, indicating a similarity to both species and confirming results of the phenogram of correlation coefficients and average taxonomic

distance. Moreover, NANU and CALB are linked, whereas THER and OCCP link with the LEON group, confirming results of the phenogram of average taxonomic distance (Fig. 15).

The subsets procedure used indicated the existence of three groups; NANU and CALB, THER and OCCP; and the LEON, BRAC, OCHR complex. The low stress value of 0.003 and the high correlation of 0.998 between the matrix of distances implied by MDSCALE and the matrix of original taxonomic distance indicate an excellent representation of the phenetic relationships as shown by the PCA/MDSCALE configuration.

When females were subjected to the same PCA/MDSCALE ordination, results obtained were similar to those of males without any noticeable variation in the placement of OTU's in the 3-D configuration (Fig. 17). However, a slight difference is apparent in the relative heights of the projections of OTU's on the third component. Moreover, the MST joined THER to OCHR in contrast to OCCP joining BRAC in males. This discrepancy may be due to the sample sizes involved. Whereas five males of OCCP were used, only one female of this OTU was available. Nevertheless, the general pattern of group relationships remained unchanged.

The first three principal components accounted for 97.45 per cent of character variability (88.69% by the first component, 6.87% by the second, and 1.89% by the third). Character loadings are given in Table 10. The first component, with high loadings of characters, indicates a size

factor. LBSP with low loading separates OTU's with long pits and small pits along the first component. The same character (LBSP) projects a high negative loading on the second component, indicating a reverse relationship with WBSP and 2M2P that load positively and separate NANU group, with small WBSP and 4M2P from the LEON and THER group with larger WBSP and 4M2P. Both CANH and ROWL display high positive loadings on the third component whereas 5M1P loads negatively.

MST superimposed on the PCA/MDSCALE ordination of female OTU's (Fig. 17) presented a pattern similar to that of male OTU's. Moreover, subsets procedures produced an identical pattern of groupings: NANU grouped with CALB, THER with OCCP, and LEON with OCHR and BRAC. A perfect stress value of 0.0 and a matrix correlation of 0.996 were obtained.

Fig. 12

Phenogram of correlation coefficients of males. The cophenetic correlation coefficient is 0.819. Refer to text for explanation of abbreviations.

Fig. 12

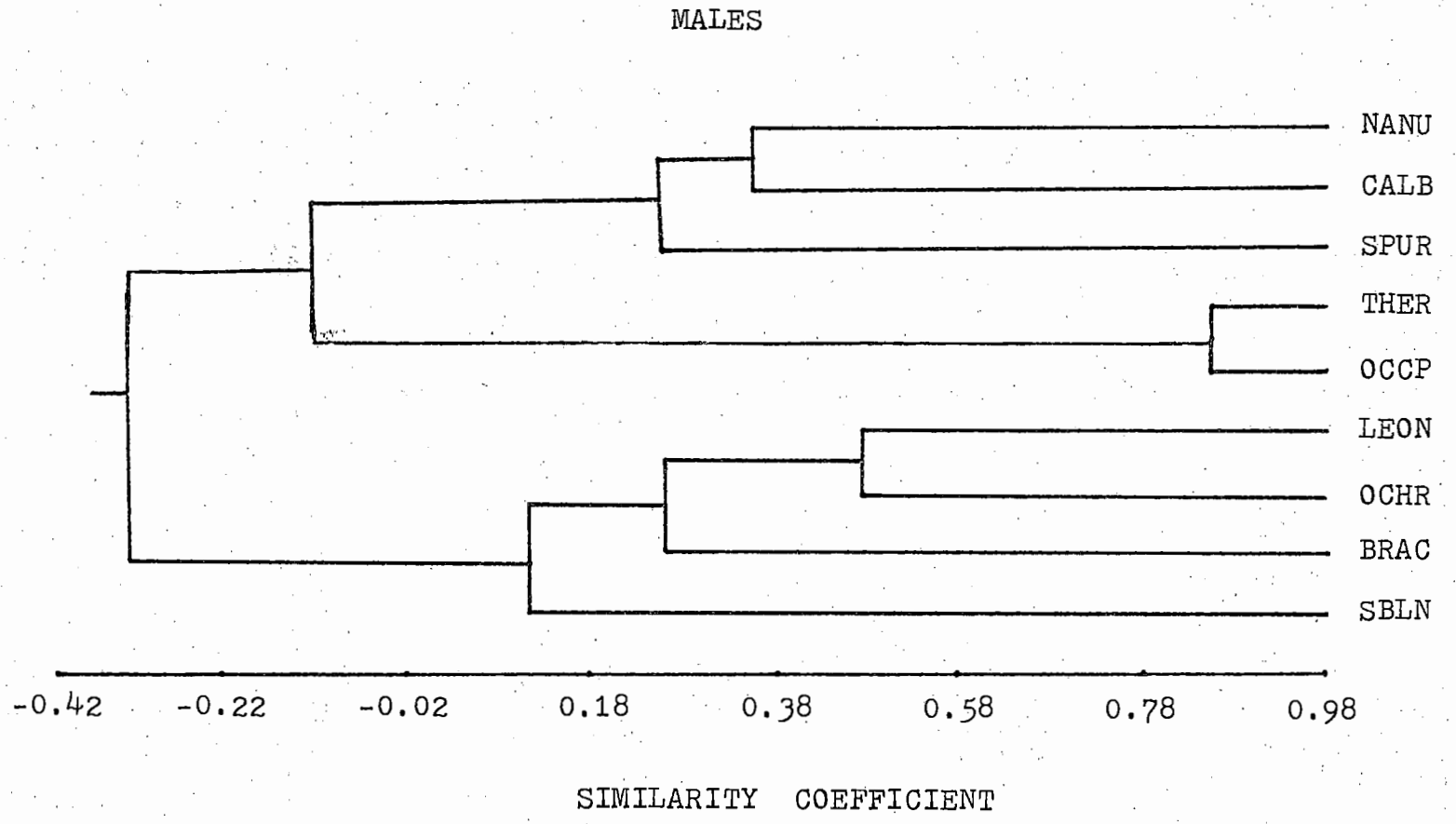

MALES
NANU
CALB
SPUR
THER
OCCP
LEON
OCHR
BRAC
SBLN
-0.42
-0.22
-0.02
0.18
0.38
0.58
0.78
0.98
SIMILARITY COEFFICIENT

Fig. 13

Phenogram of correlation coefficients of females. The cophenetic correlation coefficient is 0.896. Refer to text for explanation of abbreviations.

Fig. 13

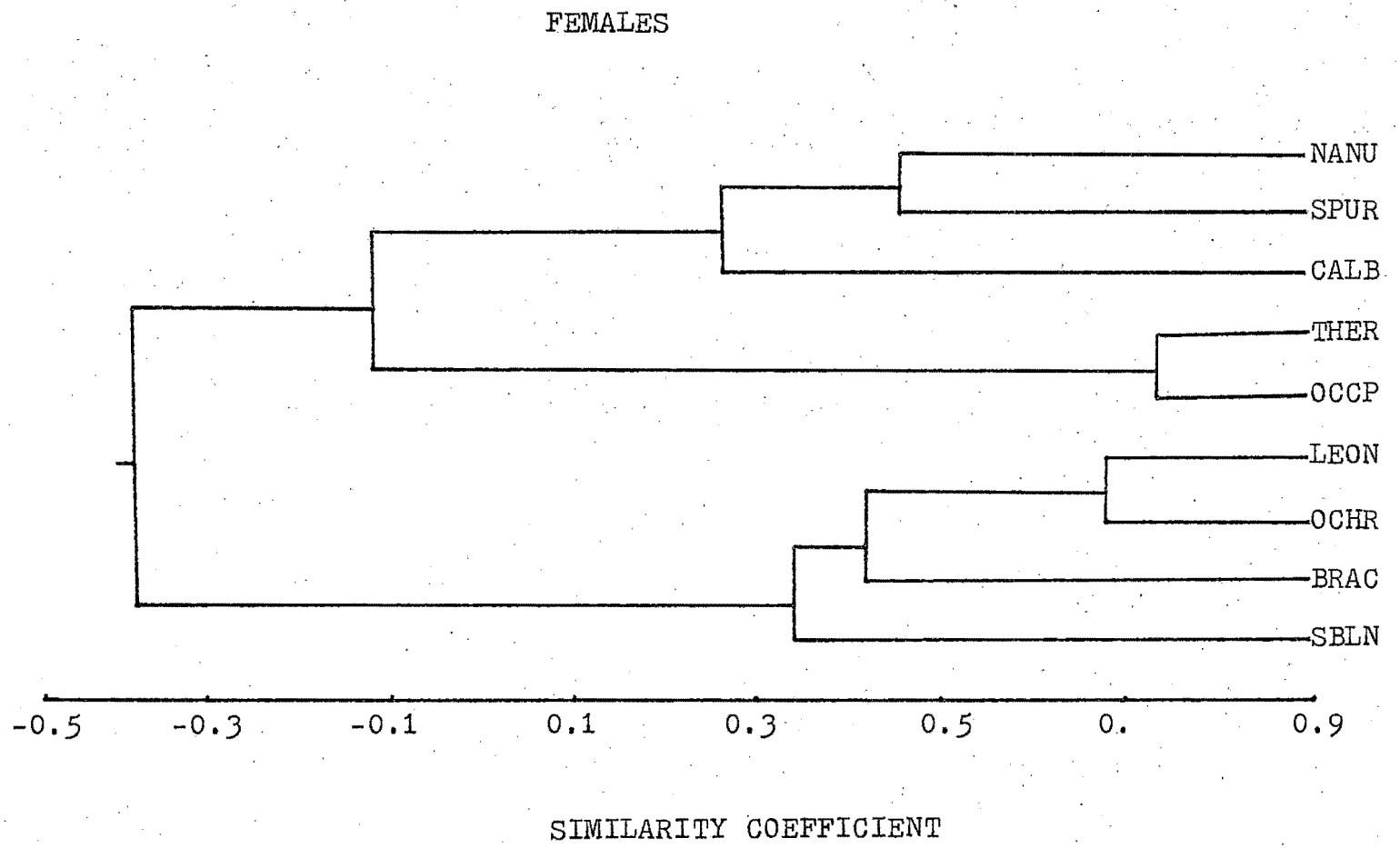

FEMALES
NANU
SPUR
CALB
THER
OCCP
LEON
OCHR
BRAC
SBLN
-0.5
-0.3
-0.1
0.1
0.3
0.5
0.
0.9
SIMILARITY COEFFICIENT

Fig. 14

Phenogram of average taxonomic distance of males. The cophenetic correlation coefficient is 0.955. Refer to text for explanation of abbreviations.

Fig. 14

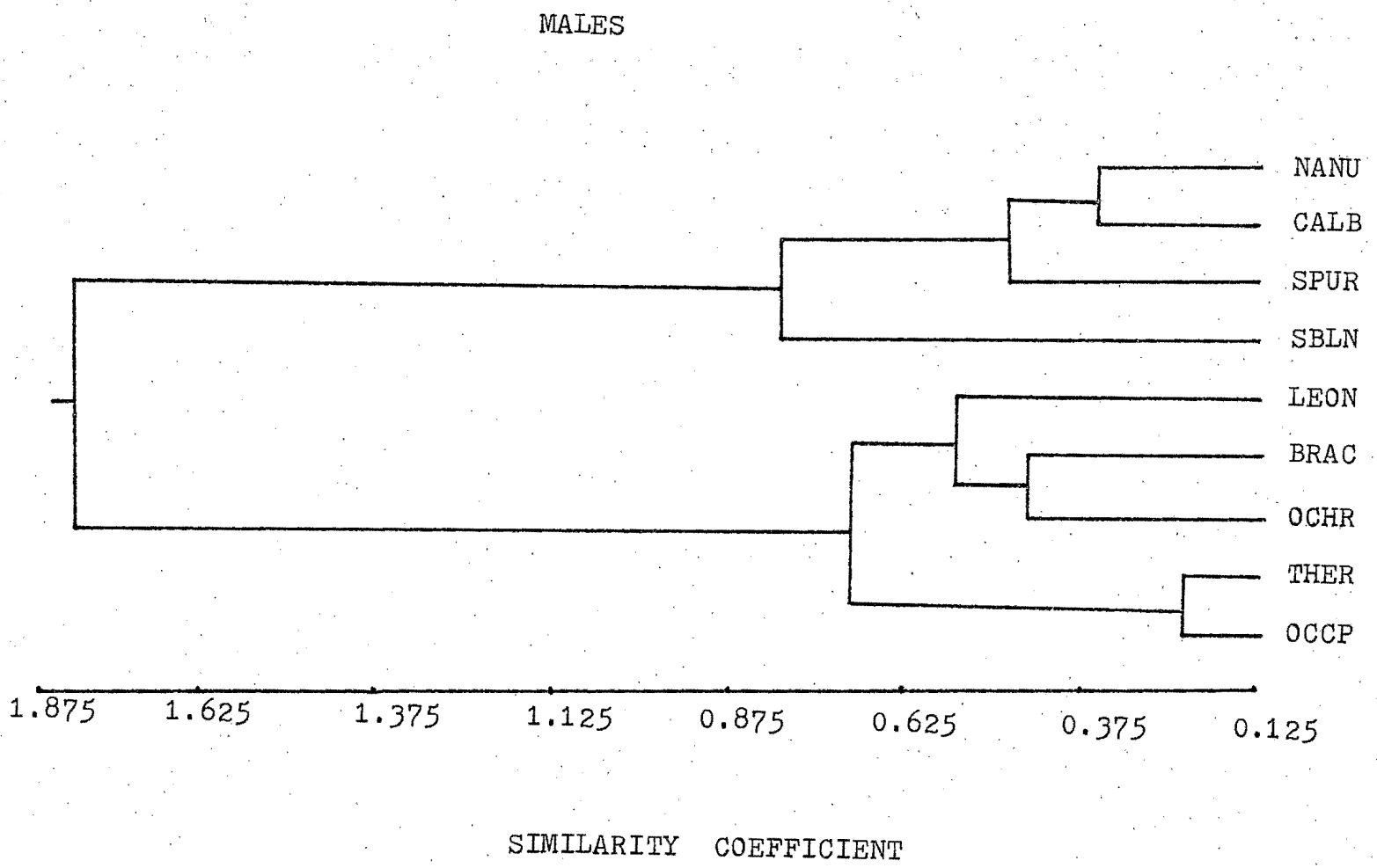

MALES
NANU
CALB
SPUR
SBLN
LEON
BRAC
OCHR
THER
OCCP
1.875
1.625
1.375
1.125
0.875
0.625
0.375
0.125
SIMILARITY COEFFICIENT

Fig. 15

Phenogram of average taxonomic distance of females. The cophenetic correlation coefficient is 0.911. Refer to text for explanation of abbreviations.

Fig. 15

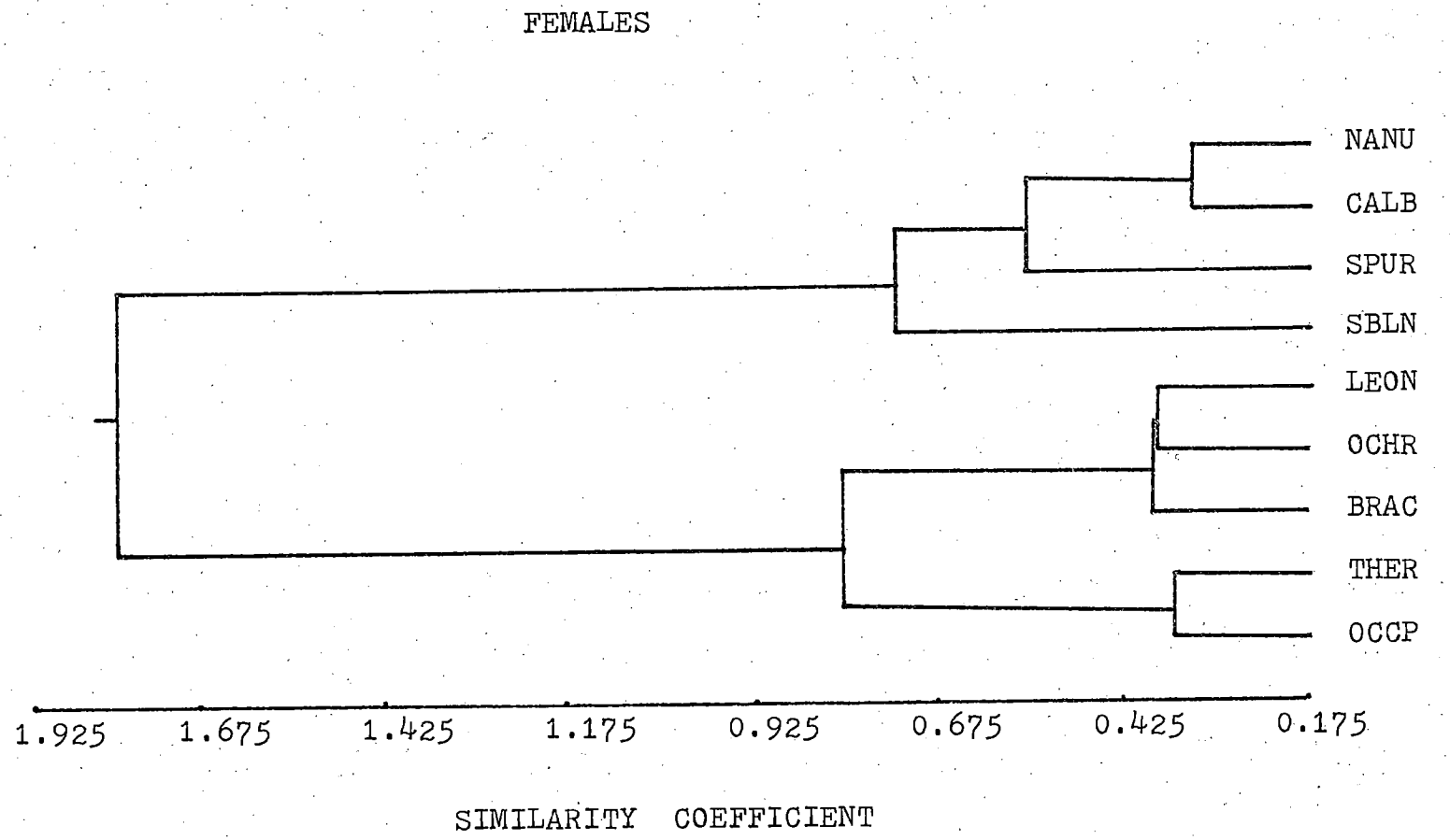

FEMALES
NANU
CALB
SPUR
SBLN
LEON
OCHR
BRAC
THER
OCCP
1.925
1.675
1.425
1.175
0.925
0.675
0.425
0.175
SIMILARITY COEFFICIENT

Fig. 16

Three-dimensional configuration for OTU's of males using PCA/MDSCALE method. Component I and II are shown whereas component III is represented by the height of the projections. Stress is denoted by s and the matrix correlation by r_{dd*}. A minimum spanning tree is indicated by broken lines joining phenetically--similar OTU's. Subsets are enclosed in solid lines. Refer to text for explanation of abbreviations.

Fig. 16

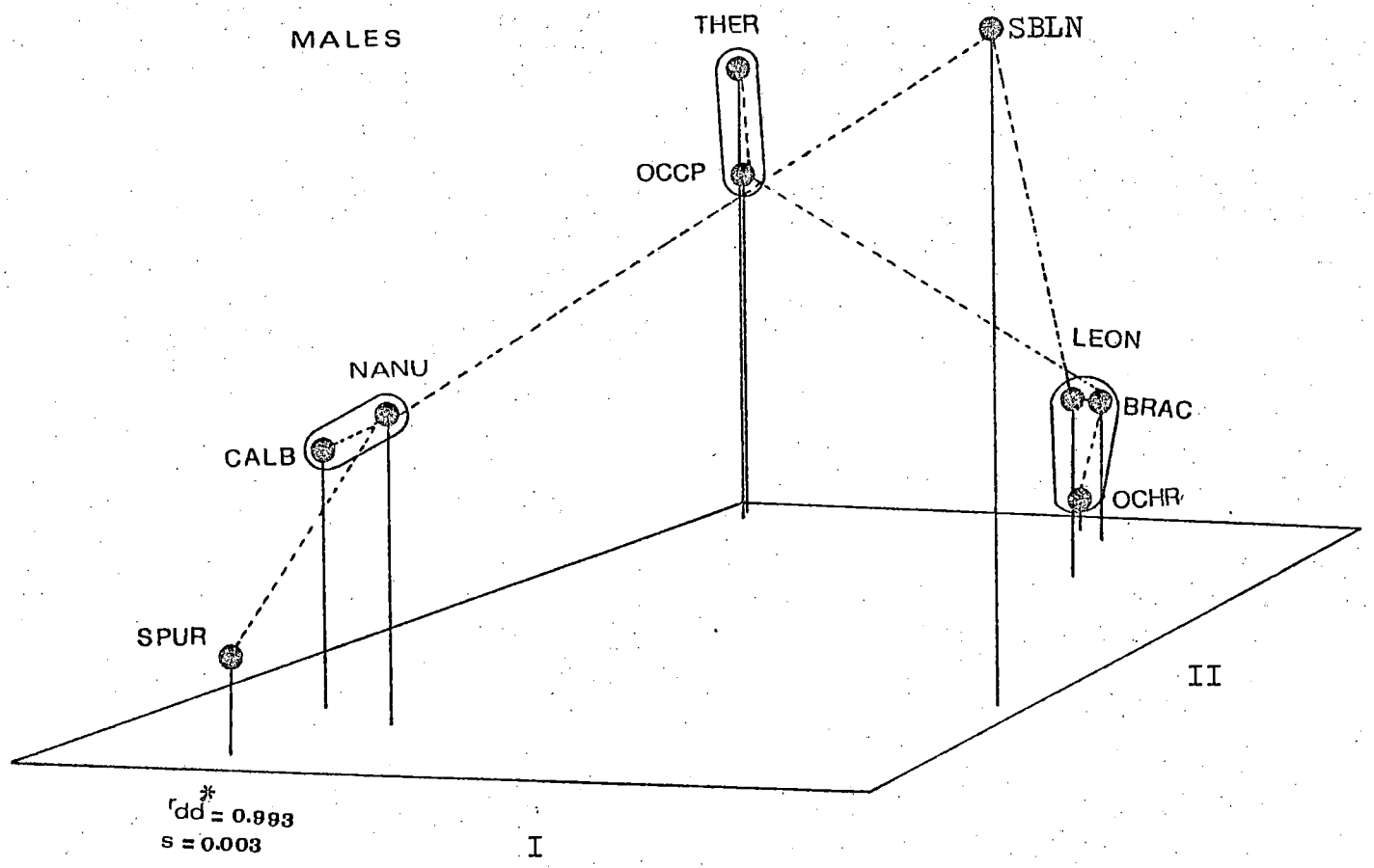

MALES
THER
SBLN
OCCP
LEON
NANU
BRAC
CALB
OCHR
SPUR
II
r^*_{dd} = 0.993
s = 0.003
I

TABLE 9

Character loadings on the first three principal components computed from the character correlation matrix of nine male Tadarida (Xiphonycteris) OTU,s. See text for character abbreviations.

Character	Components		
	1	2	3
FOAR	0.973	-0.179	0.140
3MET	0.976	-0.166	0.137
3M1P	0.982	-0.018	0.179
3M2P	0.988	-0.060	0.110
4MET	0.983	-0.137	0.122
4M1P	0.952	0.060	0.267
4M2P	0.859	0.303	0.382
5MET	0.986	-0.077	0.126
5M1P	0.962	-0.174	0.186
5M2P	0.945	-0.110	-0.071
GSLN	0.980	-0.083	0.027
CDIN	0.988	-0.096	0.014
PALL	0.994	0.008	-0.030
ZYGO	0.991	-0.124	0.020
MAST	0.990	-0.056	0.063
BBCS	0.990	-0.121	0.027
HBCS	0.848	-0.417	0.191
ROWL	0.971	0.078	-0.113
IOWA	0.928	0.104	-0.326
POCN	0.876	0.120	0.008
M3M3	0.980	-0.004	0.001
CANM	0.954	0.018	-0.275
CANC	0.969	0.078	-0.170
CANH	0.894	0.240	-0.221
WBSP	0.667	0.648	0.282
LBSP	0.346	-0.862	-0.313
CNIL	0.998	0.098	-0.001
GMLN	0.987	0.055	0.088
LCAM	0.931	0.054	-0.340
LCAC	0.935	0.236	-0.189
LCAH	0.717	0.363	-0.584

Fig. 17

Three-dimensional configuration for OTU's of females using PCA/MDSCALE method. Component I and II are shown whereas component III is represented by the height of the projections. Stress is denoted by s and the matrix correlation by r_{dd*}. A minimum spanning tree is indicated by broken lines joining phenetically--similar OTU's. Subsets are inclosed in solid lines. Refer to text for explanation of abbreviations.

Fig 17

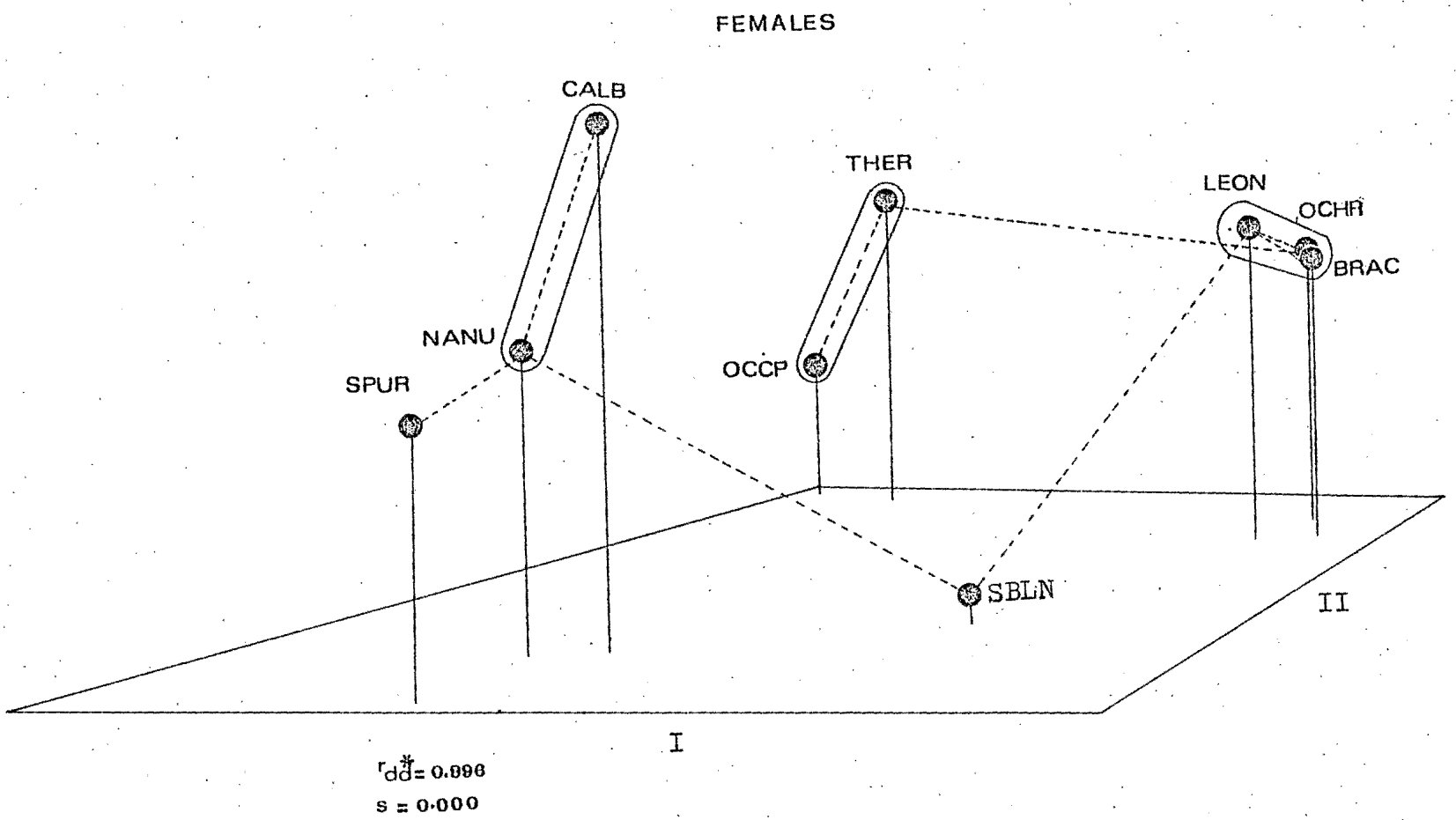

FEMALES
CALB
THER
LEON
OCHR
BRAC
NANU
SPUR
OCCP
SBLN
II
I
r_{dd}^{*}= 0.996
s = 0.000

TABLE 10

Character loadings on the first three principal components computed from the character correlation matrix of nine female Tadarida (Xiphonycteris) OTU,s. See text for character abbreviations.

Character	Components		
	1	2	3
FOAR	0.979	-0.132	-0.107
3MET	0.980	-0.009	-0.184
3M1P	0.989	0.094	-0.108
3M2P	0.984	0.120	-0.108
4MET	0.932	-0.015	-0.167
4M1P	0.977	0.164	-0.113
4M2P	0.837	0.536	-0.026
5MET	0.985	0.053	-0.151
5M1P	0.967	0.066	-0.230
5M2P	0.940	0.025	-0.132
GSLN	0.984	-0.174	0.022
CDIN	0.989	-0.132	-0.002
PALL	0.996	-0.049	-0.026
ZYGO	0.992	-0.059	0.007
MAST	0.980	-0.062	0.125
BBCS	0.987	-0.097	-0.004
HBCS	0.906	-0.309	-0.223
ROWL	0.914	-0.241	0.281
IOWA	0.909	0.241	0.075
POCN	0.912	0.211	0.193
M3M3	0.992	-0.065	0.044
CANM	0.986	-0.085	0.078
CANC	0.985	0.065	-0.080
CANH	0.941	-0.018	0.269
WBSP	0.683	0.641	0.188
LBSP	0.225	-0.958	0.022
CNIL	0.995	0.051	0.067
GMLN	0.996	-0.018	-0.016
LCAM	0.981	-0.074	0.122
LCAC	0.961	0.040	0.076
LCAH	0.923	-0.294	0.216

Geographic Variation

NANU [*T.*(*X.*) *nanula*] complex

The sample size for males of this species was so small that only geographic variation in females could be studied. Specimens were grouped into five geographical regions regarded arbitrarily as localities. The Cameroun population known as *T.*(*X.*) *calabarensis* was considered a distinct locality. Specimens from Yambio, Sudan, were grouped with specimens from Niangara, Zaire, as the two localities are contiguous (less than 130 km. apart) and are not separated by obvious geographical barriers. The number of specimens examined in each locality was as follows:

NIAN	(Niangara)	5
UGAN	(Uganda)	29
KENA	(Kenya)	17
BENN	(Benin)	5
CAMR	(Cameroun)	11

Although samples from NIAN and BENN are small, they were all that was available at the time. Few specimens from these localities are available in museum collections. Moreover, substantial sexual dimorphism in these taxa made pooling of males and females inappropriate to increase sample sizes. Nevertheless, it was necessary to use these samples because NIAN contains the type locality of *T. nanula* and BENN represents the western limit of the range of the species.

Analysis of variance detected statistically significant differences among localities in 23 characters ($P < 0.05$). Results of analyses using ranked means revealed that some characters show a general pattern of gradual increase along a west-east line, e.g., 5MET and CANC. However, this trend is reversed for CDIN, ZYGO and CNIL (Table 11). Other characters, as exemplified by PALL, do not show a clear trend.

Multivariate analysis of variance (MANOVA), which considers variation in all characters simultaneously, indicated that statistically significant differences existed among localities (F transformation of Wilks' Lambda = 2.52; df=124 and 130; $P < 0.001$). Accordingly, a generalized discriminant function analysis was performed and it produced only two significant canonical axes ($P < 0.05$) that jointly explained 84.64 per cent of the total variations among samples (55.95% by the first axis and 28.69% by the second). Samples were therefore plotted on a two-dimensional diagram (Fig. 18). The East African samples KENA and UGAN are separated from the NIAN, BENN and CAMR samples along the first canonical axis by differences in CDIN, 4M2P and to a lesser extent, PALL (Fig. 18, Table 12). Whereas BENN and CAMR fall into a cohesive morphometric unit with overlapping confidence circles and centroids connected by MST, KENA and UGAN, although connected by MST, are separated along the second canonical axis by differences in CANM and 3MET.

MST also connected NIAN with BENN instead of CAMR which is geographically closer to NIAN. However, NIAN is connected to UGAN by MST. NIAN also occupies an intermediate position between East African samples (KENA and UGAN) and West African samples (CAMR and BENN) along the first canonical axis.

The MST of the $\sqrt{D^2}$ values was superimposed on the map of geographic locations to illustrate the relationship between morphological and geographical distances among samples (Fig. 19). It is obvious that the geographic sequence is broken when NIAN links to BENN instead of CAMR.

Table 11

Tadarida nanula females

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 11

5MET

UGAN	20.33
KENA	20.32
NIAN	19.84
CAMR	19.55
BENN	19.42

CANC

UGAN	4.21
NIAN	4.09
KENA	4.07
CAMR	3.97
BENN	3.93

CDIN

CAMR	14.88
BENN	14.76
UGAN	14.76
NIAN	14.49
KENA	14.32

PALL

UGAN	6.47
NIAN	6.43
BENN	6.33
CAMR	6.27
KENA	6.10

ZYGO

CAMR	10.20
BENN	10.14
UGAN	10.10
NIAN	9.93
KENA	9.74

CNIL

CAMR	11.04
BENN	10.95
UGAN	10.87
NIAN	10.83
KENA	10.55

Fig. 18

Bivariate plots of canonical axis I against canonical axis II for localities of female T. nanula complex. Locality centroids are enclosed by 95 % confidence circles. A minimum spanning tree connecting locality centroids is shown by broken lines. Contributions of individual characters to the separation of locality centroids are indicated by magnitude and direction of the character vectors, which are scaled relative to the pooled within group standard deviations. For clarity only those characters with the largest vectors are selected. Refer to text for explanation of abbreviations.

Fig. 18

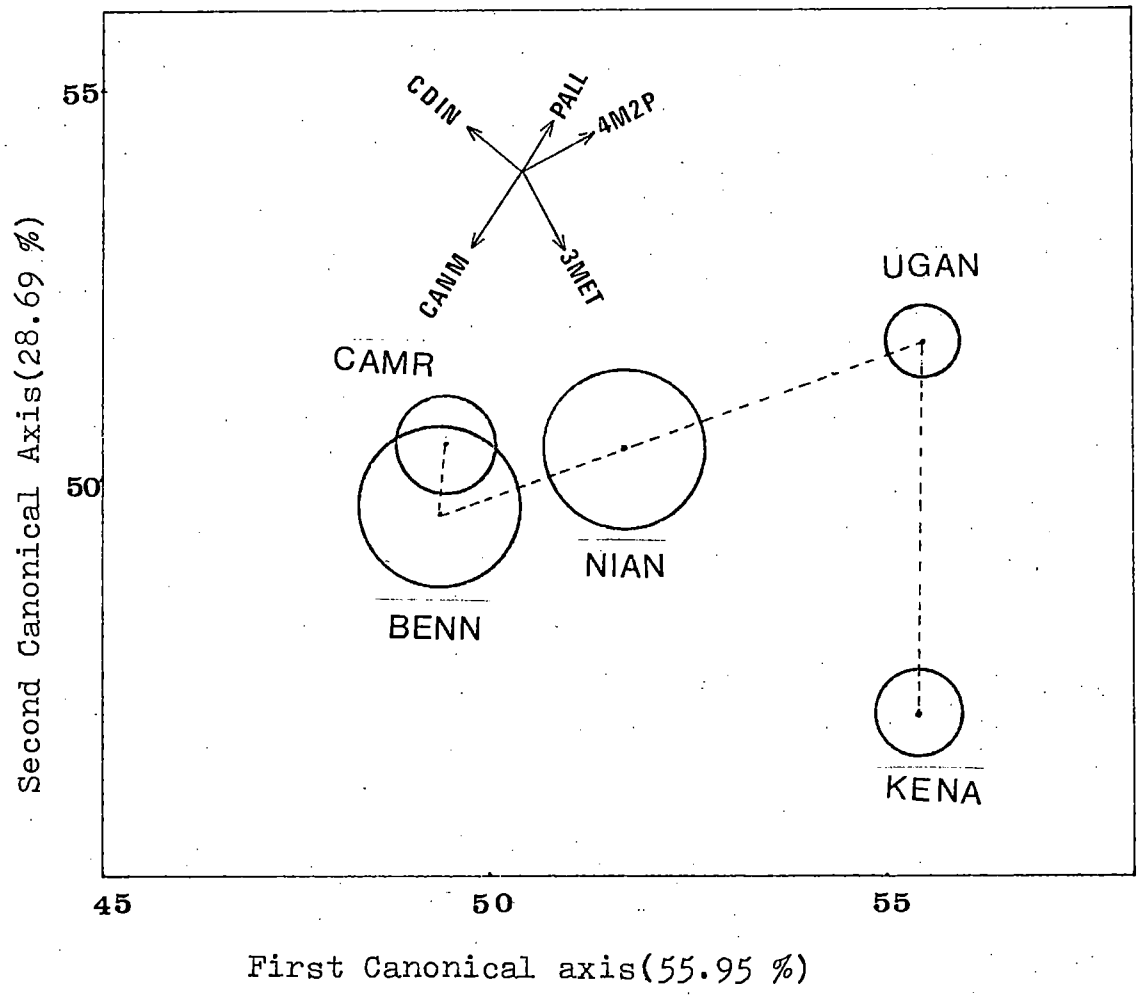

55
50
45
50
55
Second Canonical Axis(28.69 %)
First Canonical axis(55.95 %)
CDIN
PALL
4M2P
CANM
3MET
CAMR
UGAN
NIAN
BENN
KENA

TABLE 12

Character loadings on the first two canonical axes of localities of female T. nanula. See text for character abbreviations.

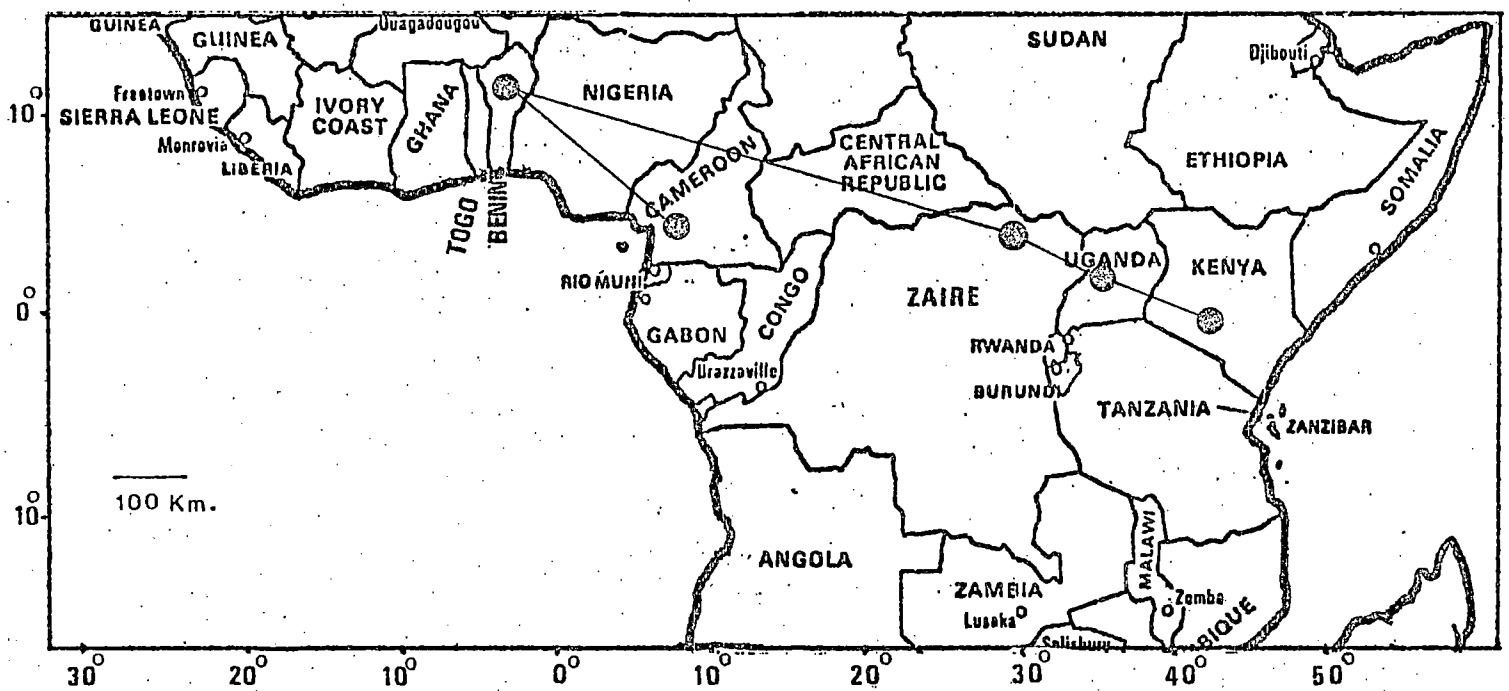
Character	Canonical Axes	
	1	2
FOAR	0.0978	0.0170
3MET	0.3185	-1.1088
3M1P	-0.2187	-0.8004
3M2P	-0.1495	-0.3252
4MET	0.0420	1.1221
4M1P	-0.5511	-0.4308
4M2P	1.0576	0.4287
5MET	1.0333	0.0093
5M1P	0.3138	-0.1724
5M2P	0.5167	-0.1630
GSLN	0.3861	0.3702
CDIN	-0.5944	0.5504
PALL	0.5033	0.6486
ZYGO	0.0882	0.2474
MAST	0.1868	0.2439
BBCS	0.0969	0.2485
HBCS	-0.0684	-0.2577
ROWL	-0.3226	0.1214
IOWA	0.1594	-0.2539
POCN	0.6297	-0.1969
M3M3	0.0555	0.2515
CANM	-0.7735	-0.8071
CANC	0.6884	0.2731
CANH	-0.1556	0.3427
WBSP	0.4062	-0.1828
LBSP	0.3186	0.2520
CNIL	0.0032	-0.4542
GMLN	-0.2082	-0.7044
LCAM	0.1919	0.5160
LCAC	-0.7933	0.1437
LCAH	-0.4317	0.0888

*Scaled vectors X pooled within-group standard deviations.

Fig. 19

A minimum spanning tree of the square root of the Mahalanobis' distance values superimposed on a map of geographic locations of samples of female T. nanula complex.

Fig. 19


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
SUDAN
Djibouti
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
ETHIOPIA
SOMALIA
UGANDA
KENYA
RIO MUNI
GABON
CONGO
ZAIRE
RWANDA
BURUNDI
Brazzaville
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
Lusaka
MALAWI
Zomba
Salisbury
MOZAMBIQUE
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

LEON [T.(X.) leonis] comples -- males

In this study, males and females of this complex were treated separately. Despite small samples, I tried to examine general trends of geographic variation among samples using available material. Males of this complex were grouped into four localities. Specimens from adjacent localities or regions were sometimes grouped together. As the aim of the study is to investigate the morphologic relationships among the Western, the Central and the Eastern African populations, specimens from Sierra Leone and Ghana were grouped into a West African population (WAFR). Sierra Leone contains the type locality for bats described by Thomas (1908) as T. leonis. Specimens from Medje (Zaire) described by Allen (1917) as T. ochraceus are referred to by the name of the type locality. Specimens housed in the ROM from the Budongo Forest (Uganda) and identified as T. brachyptera were compared with the other samples. Localities were represented as follows:

WAFR	(West Africa)	30
CAMR	(Cameroun)	5
MEDJ	(Medje)	4
UGAN	(Uganda)	6

Univariate analysis of variance detected significant differences among locality samples in 22 characters ($P < 0.05$). It also detected a gradual increase in wing and skull measurements along a west-east cline. The

sample from WAFR had the smallest measurements (Table 13) and is significantly smaller than other samples in three characters (3MET, 5MET and 5M2P). In other characters it occurs with the CAMR sample in nonsignificant subsets (Table 14).

MANOVA showed that samples differed significantly (F transformation of Wilks' Lambda = 5.79, df=93 and 34, $P < 0.001$). A generalized discriminant analysis generated three significant axes ($P < 0.05$) that explain 53.52, 35.92 and 10.56 per cent of character variation among samples (total of 100%).

Three-dimensional projections of the samples are shown in Fig. 20. A MST superimposed on the diagram linked WAFR and CAMR. Although MEDJ linked with UGAN, CAMR linked with UGAN instead of MEDJ, a relation difficult to explain geographically but could be due to small unrepresentative samples. The subsets procedure produced a single subset grouping, UGAN and CAMR.

Character loading (Table 15) on the first canonical axis showed that CNIL, while loading negatively, contributes highly in the separation of samples along the first axis, whereas 3MET, with a positive loading, also contributes but to a lesser degree. Along the second axis samples are separated by 4MET and GSLN. Samples are also separated along the third axis by 5MET and CDIN (Fig. 20).

MST was superimposed on the map of geographic locations of samples and a slightly distorted geographic sequence is indicated by the connection of CAMR and UGAN (Fig.21).

Table 13

T. leonis complex - males

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 13

FOAR

MEDJ	38.37
UGAN	38.22
CAMR	37.42
WAFR	36.38

3MET

MEDJ	40.17
UGAN	40.14
CAMR	39.67
WAFR	38.04

4MET

MEDJ	38.42
UGAN	38.29
CAMR	37.86
WAFR	36.71

5MET

CAMR	26.39
MEDJ	26.05
UGAN	25.87
WAFR	24.58

5M1P

MEDJ	10.55
UGAN	10.47
CAMR	9.99
WAFR	9.57

5M2P

MEDJ	3.75
CAMR	3.70
UGAN	3.63
WAFR	3.21

Table 14

T. leonis complex - males

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 14

GSLN

UGAN	19.84
CAMR	19.23
WAFR	19.05
MEDJ	19.00

CDIN

UGAN	18.26
CAMR	17.89
MEDJ	17.85
WAFR	17.38

ZYGO

MEDJ	12.37
CAMR	12.36
UGAN	12.18
WAFR	11.90

MAST

UGAN	11.32
MEDJ	11.24
CAMR	11.22
WAFR	10.84

BBCS

MEDJ	9.82
UGAN	9.78
CAMR	9.73
WAFR	9.42

ROWL

UGAN	7.05
MEDJ	6.81
CAMR	6.76
WAFR	6.64

Fig. 20

Three-dimensional diagram of sample localities of T. leonis males. Localities are projected on the canonical axes I, II and III (the height of the projections). Localities are connected by a minimum spanning tree of Mahalanobis' $\sqrt{D^2}$ values, shown here by broken lines. Subsets are inclosed in solid lines. Refer to text for explanation of abbreviations.

Fig. 20

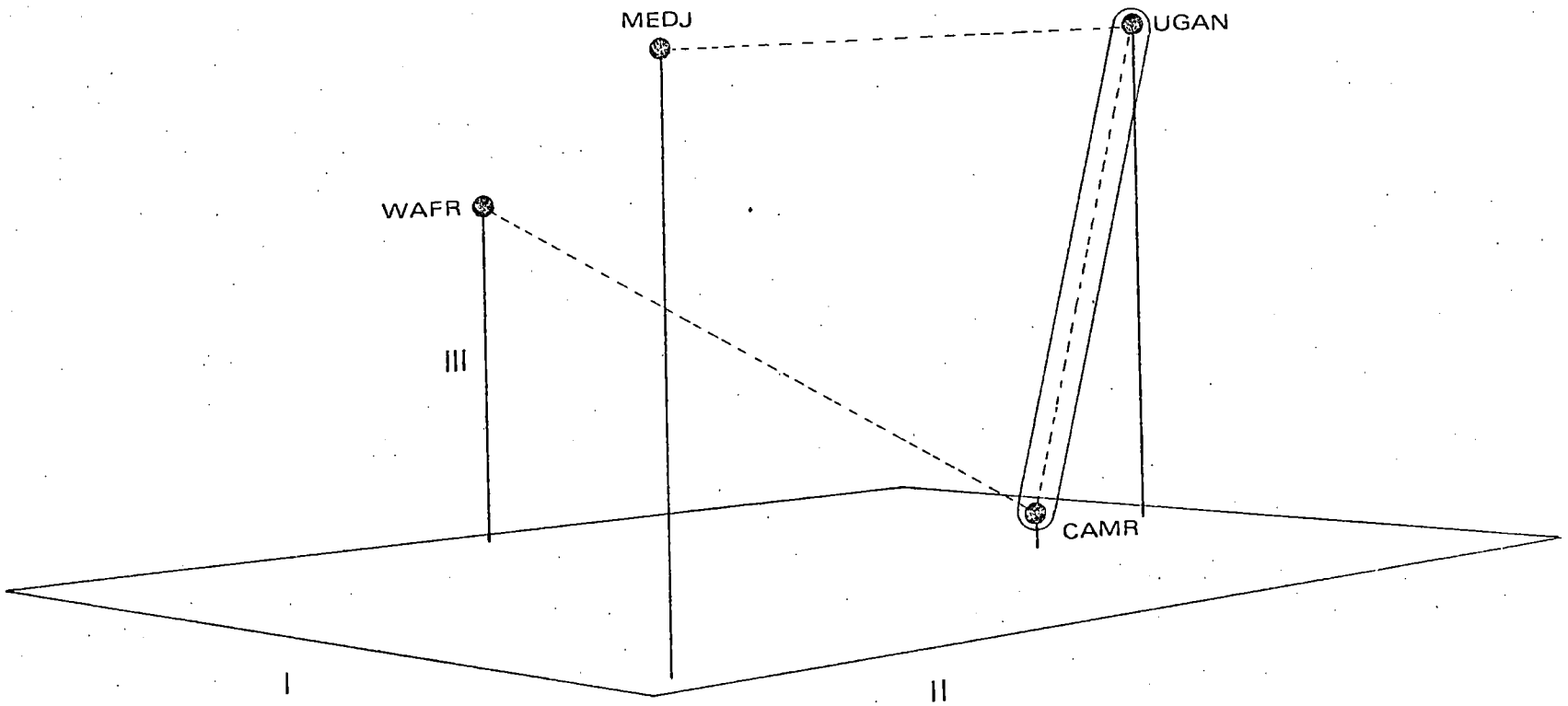


TABLE 15

Character loadings* on the first three canonical axes of localities of male T. leonis. See text for character abbreviations.

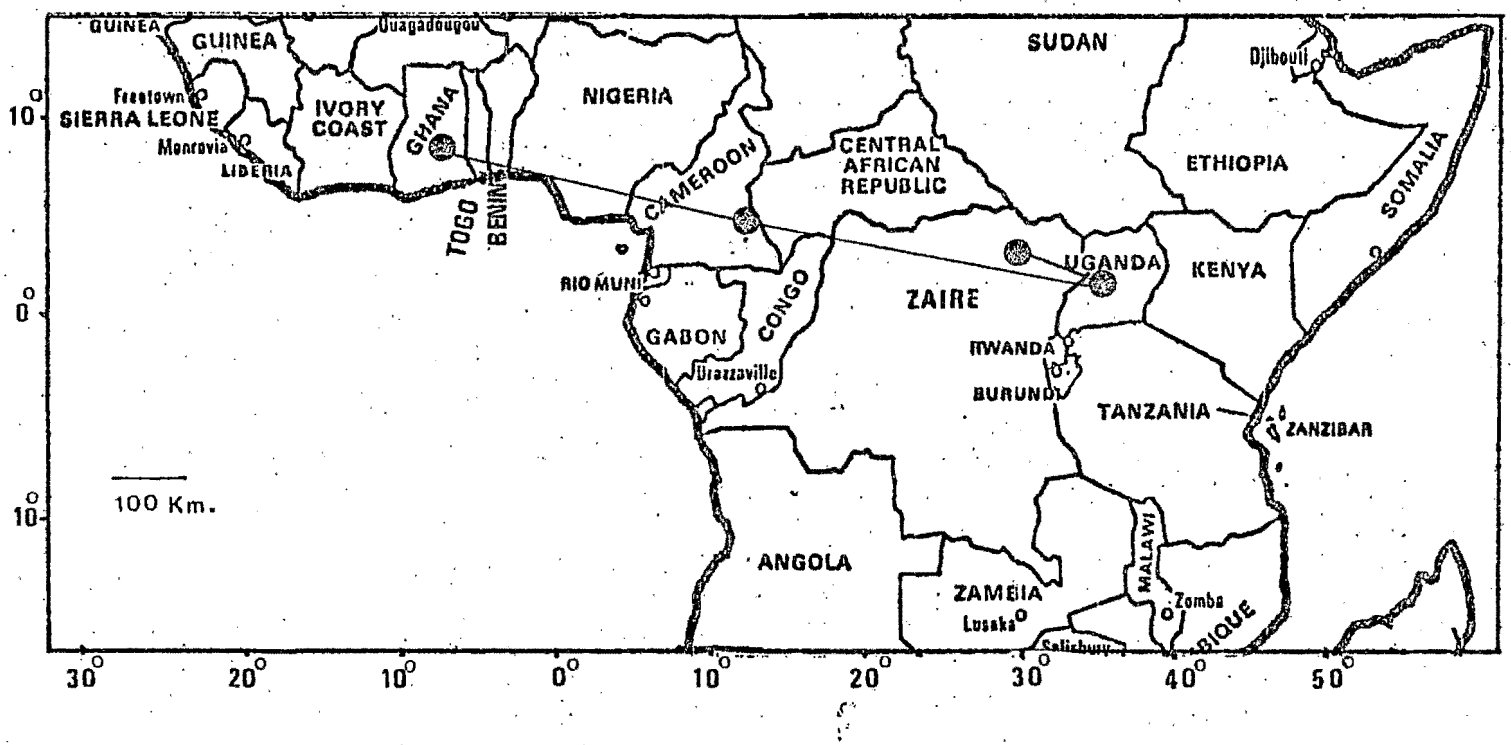
Character	Canonical Axes		
	1	2	3
FOAR	-0.3153	0.6439	1.1541
3MET	2.6932	-2.8431	-0.2644
3M1P	1.1421	0.3868	0.2735
3M2P	-0.3251	0.0240	-0.0107
4MET	-2.2108	4.9826	1.2510
4M1P	-0.0387	-1.6708	1.0455
4M2P	-0.1245	0.0809	-1.1405
5MET	1.4812	-0.9067	-2.6350
5M1P	-0.4628	0.4078	0.6439
5M2P	1.5497	0.5904	0.2508
GSLN	-1.2096	3.2059	-1.7278
CDIN	2.5705	2.8320	2.3935
PALL	0.9656	-2.6366	1.1174
ZYGO	0.6638	-1.1986	-1.8737
MAST	-2.0200	2.7236	0.1888
BBCS	1.4120	-0.5422	0.3177
HBCS	0.3128	-0.0987	0.5003
ROWL	0.3369	-0.7601	-0.5653
IOWA	0.6873	-1.2870	0.1032
POCN	2.2489	-1.0266	-0.7683
M3M3	0.4339	1.1114	0.6408
CANM	-0.4672	0.6982	0.6246
CANC	0.1777	-1.3974	0.7470
CANH	0.1069	-1.2080	-0.4893
WBSP	0.3861	0.1742	0.0594
LBSP	-0.3677	-0.1031	-0.0861
CNIL	-3.3265	1.1397	-0.8950
GMLN	-1.9786	-2.9010	-0.2013
LCAM	-0.8829	-1.3621	0.5607
LCAC	1.8517	0.1332	-0.6554
LCAH	-2.4645	-1.9995	-1.0119

*Scaled vectors X pooled within-group standard deviations.

Fig. 21

A minimum spanning tree of the square root of the Mahalanobis' distance values superimposed on a map of geographic locations of samples of male T. leonis complex.

Fig. 21


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
SUDAN
Djibouti
ETHIOPIA
SOMALIA
RIO MUNI
GABON
CONGO
Brazzaville
ZAIRE
UGANDA
KENYA
RWANDA
BURUNDI
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
Lusaka
MALAWI
Zomba
Salisbury
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

LEON [T.(X.) leonis] complex -- females

Female samples were represented by specimens from the same geographic localities as males, as follows:

WAFR	51
MEDJ	15
CAMR	4
UGAN	4

Samples from CAMR and UGAN were so few that only general statements of their relationship to specimens from the other two localities are made. Nonetheless, anlaysis of variance detected statistically significant differences among localities in 21 characters ($P < 0.05$). In all but seven characters (3MET, 3M2P, 4MET, 5M1P, HBCS, POCN, and GMLN), the WAFR sample is smaller than other samples.

Table 16 gives selected character means arranged in decreasing order. The general trend suggests that there is an increase in character size towards the Central and East African regions and that the West African sample is the smallest in size.

Considering all characters simultaneously, MANOVA showed that there are significant differences among locality samples ($F = 5.06$; $df=93$ and 121; $P < 0.001$). The generalized discriminant function analysis that followed the MANOVA test produced three statistically significant axes ($P < 0.01$) that explain 75.46, 13.54 and 11.01 per cent of character variation among samples (total of 100%).

Results of the generalized discriminant anlaysis are illustrated in Fig. 22. MST superimposed on the 3-D configuration linked WAFR with MEDJ, MEDJ with CAMR and UGAN. The subsets procedure grouped together MEDJ and UGAN, indicating that the similarity between the two samples is greater than the similarity of any one of the two samples and the CAMR or WAFR samples. On the other hand, MEDJ is linked by MST to CAMR in a sequence that is geographically acceptable, but the link between MEDJ and WAFR is difficult to explain. It would have been more logical if CAMR and WAFR were linked because of their close geographic proximity. This is probably caused by the small samples for CAMR and UGAN.

In general terms, it is apparent from the above results that the Central and Eastern African samples are closely linked whereas the Western African samples are weakly linked to the other samples. This is indicated by the low correlation value of 0.326 between the $\sqrt{D^2}$ matrix and MST.

Character loading on the three canonical axes given in Table 17 help to explain the dispersion of sample localities in Fig. 22. The 5M2P shows a high negative loading on the first axis, as do ZYGO and 4MET, but to a lesser degree. These characters help to separate the Central and East African localities (CAMR, MEDJ and UGAN) from WAFR samples along the first canonical axis. The

Central and East AFrican localities (CAMR, MEDJ and UGAN) are separated along the second axis by CNIL and CANM. Differences in BBCS, CDIN and CNIL help to separate UGAN from other localities along the third axis.

MST, superimposed on the map of geographic locations is given in Fig. 23. A distortion in geographic sequence is noticeable in the connection between WAFR and MEDJ samples.

Table 16

Tadarida leonis complex - females

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 16

3M1P

MEDJ	15.34
CAMR	14.81
UGAN	14.70
WAFR	14.35

5MET

CAMR	25.55
MEDJ	25.55
UGAN	24.90
WAFR	24.40

5M2P

CAMR	3.85
MEDJ	3.46
UGAN	3.30
WAFR	3.08

GSLN

CAMR	18.99
MEDJ	18.56
UGAN	18.32
WAFR	18.18

BBCS

UGAN	9.42
CAMR	9.40
MEDJ	9.39
WAFR	9.12

GMLN

CAMR	13.41
MEDJ	13.16
UGAN	12.91
WAFR	12.86

Fig. 22

A three-dimensional diagram of sample localities of Tadarida leonis females. Localities are projected on discriminant functions I, II and III (the height of projections). Localities are connected by the minimum spanning tree of Mahalanobis' $\sqrt{D^2}$ values, shown here by broken lines. Subsets are enclosed in solid lines. Refer to text for explanation of abbreviations.

Fig. 22

TABLE 17

Character loadings on the first three canonical axes of localities of female T. leonis. See text for character abbreviations.

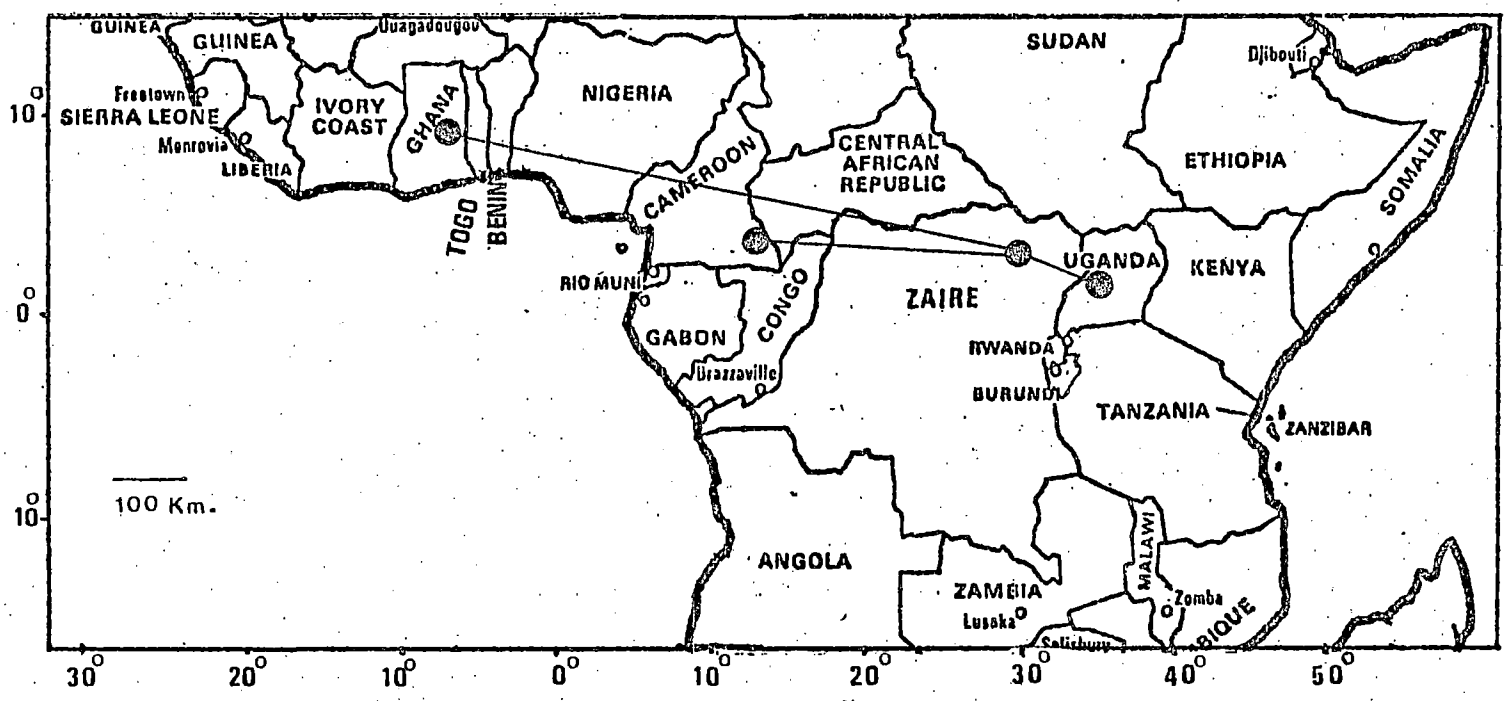
Character	Canonical Axes		
	1	2	3
FOAR	1.3683	-0.1194	0.2202
3MET	1.6702	0.0675	0.6158
3M1P	-0.2075	0.7218	0.2226
3M2P	0.1774	0.2253	-0.0211
4MET	-2.6600	0.7939	0.5875
4M1P	-0.5029	-0.5106	-0.5475
4M2P	0.6086	-0.7339	-0.0236
5MET	-0.1732	-0.5980	-0.4662
5M1P	0.1505	0.5713	0.5182
5M2P	-3.6363	0.0759	0.4410
GSLN	0.0181	0.3683	0.4020
CDIN	1.2175	0.3293	1.3655
PALL	0.3545	-0.5957	0.3108
ZYGO	-2.9776	0.6057	0.6303
MAST	-0.6237	-0.4937	-0.5751
BBCS	0.7943	-0.0719	1.3975
HBCS	0.1880	-0.0818	-0.4211
ROWL	-0.2768	0.4171	-0.5370
IOWA	0.4539	0.2889	0.0976
POCN	-0.7833	0.1818	0.5568
M3M3	1.7870	0.0054	-0.1522
CANM	-0.4549	-1.2174	0.4814
CANC	1.6638	-0.2106	0.5830
CANH	-0.6526	-0.3157	0.0107
WBSP	0.2217	0.0403	-0.1736
LBSP	-0.2575	0.2511	0.0217
CNIL	-1.7652	-2.5544	1.1246
GMLN	0.6731	0.2868	-0.1632
LCAM	0.6706	0.6576	-0.9391
LCAC	-2.7379	-0.0199	1.0342
LCAH	-0.1645	0.9936	-0.0401

*Scaled vectors X pooled within-group standard deviations.

Fig. 23

A minimum spanning tree of the square root of the Mahalanobis' distance values superimposed on a map of geographic locations of samples of T. leonis females.

Fig. 23


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
SUDAN
Djibouti
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
ETHIOPIA
SOMALIA
RIO MUNI
UGANDA
KENYA
GABON
CONGO
ZAIRE
RWANDA
Brazzaville
BURUNDI
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
MALAWI
Lusaka
Zomba
Salisbury
MOZAMBIQUE
10°
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10°
0°
10°
20°
30°
40°
50°

THER [T.(X.) thersites] complex -- males

Specimens examined represent five geographical localities. The type specimen (AMNH 48851) designated as T. occipitalis by Allen (1917) was grouped with specimens from Medje and Luluabourg, as the type locality, Avakubi, in eastern Zaire is not far from Medje. Other specimens are representatives of the species described by Thomas (1903) as T. thersites. Specimens were represented as follows:

MEDJ	5
IVCO	7
GHAN	19
CAMR	19
UGAN	16

Analysis of variance detected statistically significant differences among localities in 15 characters ($P < 0.05$). Perhaps one consistent pattern of interlocality differention emerged from the SS-STP procedure. Samples from GHAN are smaller in 11 characters whereas samples from UGAN are larger in 13 characters, and smaller than other samples in only one character, WBSP. Selected characters are given in Table 18. Samples from CAMR and UGAN have large PALL and GSLN, although they combine with samples from MEDJ and IVCO in nonsignificant subsets for these two characters. the MANOVA test indicated that statistically significant differences existed among localities

($F = 1.91$; df=124 and 126; $P < 0.001$). A generalized discriminant analysis produced two significant axes ($P < 0.05$). Accordingly, sample localities are dispersed along the first and second canonical axes that explain 47.16 and 27.96 per cent of variation among samples (total of 75.12%). Results are shown in Fig. 24. MST superimposed on the two-dimensional configuration does not indicate a geographically related pattern. Although the West African samples (GHAN, IVCO) were linked the pattern is disrupted when IVCO linked to CAMR. CAMR is geographically nearer to GHAN than to IVCO. Furthermore, CAMR was linked to UGAN and MEDJ. This pattern of relationships suggests that the MEDJ sample is morphologically more similar to the CAMR sample than to that from UGAN, although MEDJ is geographically nearer to UGAN than to CAMR (Fig. 25).

Vectors, selected by the relative contribution of characters (Table 19), indicate that the GHAN sample is separated from the UGAN sample by 4MET, PALL, 5MET and CDIN, and the UGAN is separated from CAMR, MEDJ and IVCO by differences in GSLN, WBSP, 5MET and CDIN. Moreover, GHAN is differentiated from IVCO, MEDJ and CAMR by differences in 3MET, 4MET and PALL. However, GHAN and UGAN are separated from IVCO, MEDJ and CAMR along the second canonical axis by differences in 5MET, CANH, 3MET, CANC, WBSP and GSLN.

Table 18

Tadarida thersites males

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 18

FOAR		4MET	
UGAN	39.65	UGAN	39.26
IVCO	38.99	IVCO	38.91
CAMR	37.98	MEDJ	38.68
MEDJ	37.83	GHAN	38.40
GHAN	37.75	CAMR	37.99
5MET		**GSLN**	
UGAN	27.19	UGAN	19.49
MEDJ	26.74	CAMR	19.47
IVCO	26.30	IVCO	19.46
GHAN	25.97	MEDJ	19.43
CAMR	25.89	GHAN	18.99
CDIN		**WBSP**	
UGAN	18.29	IVCO	1.36
IVCO	17.93	GHAN	1.31
CAMR	17.88	CAMR	1.28
MEDJ	17.85	MEDJ	1.27
GHAN	17.60	UGAN	1.23
BBCS		**LCAH**	
UGAN	9.86	UGAN	2.94
IVCO	9.74	MEDJ	2.90
MEDJ	9.72	CAMR	2.87
CAMR	9.66	IVCO	2.84
GHAN	9.58	GHAN	2.66

Fig. 24

Bivariate plots of canonical axis 1 against canonical axis II for localities of male T. thersites complex. Locality centroids are enclosed by 95 % confidence circles. A minimum spanning tree connecting locality centroids is shown by broken lines. Contributions of individual characters to the separation of locality centroids are indicated by magnitude and direction of the character vectors, which are scaled relative to the pooled within-group standard deviations. For clarity only those characters with the largest vectors are selected. Refer to text for explanation of abbreviations.

Fig. 24

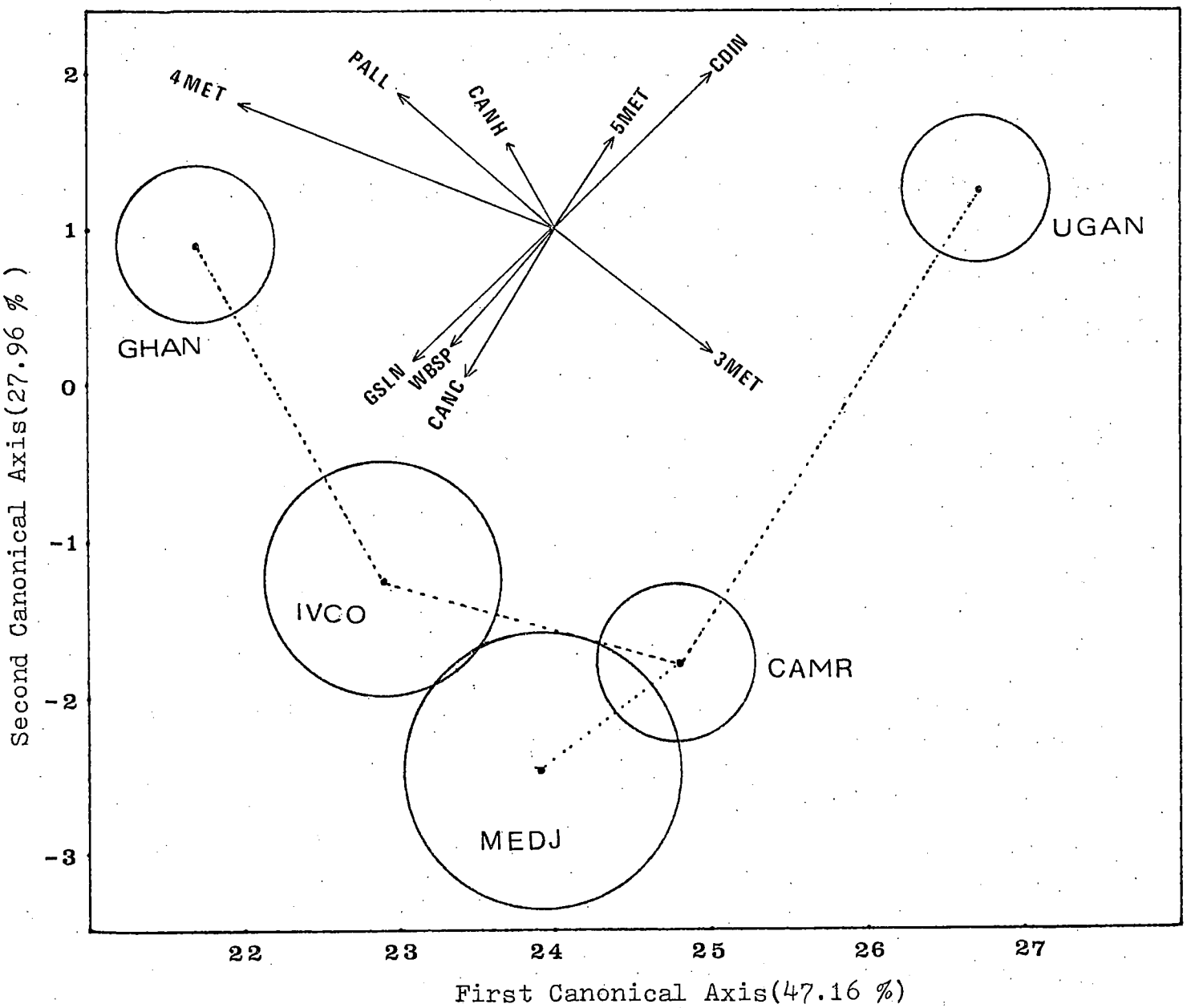

4MET
PALL
CANH
5MET
CDIN
3MET
GSLN
WBSP
CANC
GHAN
IVCO
MEDJ
CAMR
UGAN
2
1
0
-1
-2
-3
22
23
24
25
26
27
Second Canonical Axis(27.96 %)
First Canonical Axis(47.16 %)

TABLE 19

Character loadings* on the first two canonical axes of localities of male T. thersites. See text for character abbreviations.

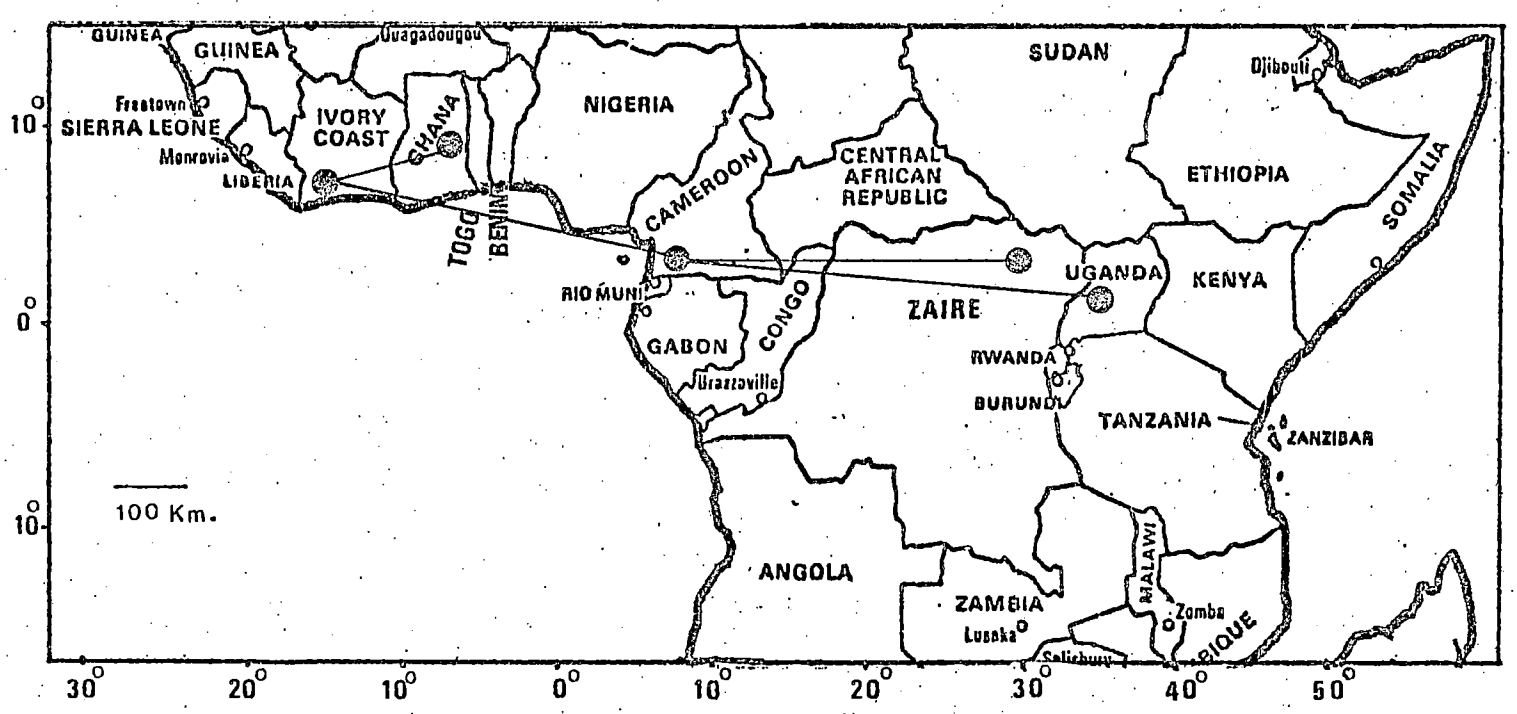
Character	Canonical Axes	
	1	2
FOAR	-0.2193	0.3017
3MET	1.1487	-0.8375
3M1P	0.4172	-0.4889
3M2P	-0.6838	-0.1232
4MET	-2.1311	0.8831
4M1P	0.4489	-0.0644
4M2P	0.2885	0.3569
5MET	0.5907	0.5644
5M1P	-0.0384	0.5830
5M2P	-0.2506	-0.4519
GSLN	-0.8919	-0.9002
CDIN	1.0615	1.0211
PALL	-0.8598	0.7650
ZYGO	-0.5242	0.3209
MAST	0.3318	0.2241
BBCS	0.2650	0.1936
HBCS	-0.1304	-0.1766
ROWL	0.5968	0.0799
IOWA	-0.7105	0.2613
POCN	0.2199	0.4955
M3M3	0.8445	0.1633
CANM	-0.8589	0,0897
CANC	-0.6434	-0.7830
CANH	-0.3160	0.5599
WBSP	-0.7850	-0.6109
LBSP	-0.3247	-0.2805
CNIL	0.4053	-0.2805
GMLN	0.2135	0.2961
LCAM	-0.0759	0.2982
LCAC	-0.3247	0.0791
LCAH	0.2889	-0.5184

*Scaled vectors X pooled within-group standard deviations.

Fig. 25

A minimum spanning tree of the square root of the Mahalanobis' distance values superimposed on a map of geographic locations of samples of T. thersites males.

Fig. 25.


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
SUDAN
Djibouti
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
ETHIOPIA
SOMALIA
RIO MUNI
UGANDA
KENYA
GABON
CONGO
ZAIRE
RWANDA
Brazzaville
BURUNDI
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
MALAWI
Lusaka
Zomba
Salisbury
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

THER [T.(X.) thersites] complex -- females

As only two females were available from MEDJ, samples were represented in this study by five localities (not including MEDJ):

IVCO	20
TOGO	5
GHAN	15
CAMR	22
UGAN	15

Analysis of variance showed that the five localities differed significantly in 20 characters ($P < 0.05$). The SS-STP procedure indicated that the UGAN sample averages larger than other samples in 12 characters, whereas the GHAN sample is smaller in 19 characters, thus supporting the pattern of interlocality differentiation shown by male sample localities. Moreover, UGAN is significantly larger than other samples in BBCS (Table 20) and does not have small WBSP as do males.

The MANOVA test detected significant differences among localities ($F = 2.39$; $df=124$ and 170; $P < 0.001$). A generalized discriminant analysis produced two significant canonical axes ($P < 0.05$) that explained 60.80 and 20.27 per cent of variation among localities (total of 81.07%). Localities were plotted against the first two axes in a two-dimensional diagram shown in Fig. 26. A MST superimposed on the configuration and on the map of geographic

locations (Fig. 27) indicates a disrupted geographic sequence in the link between CAMR and TOGO. Although CAMR is nearer to TOGO than IVCO and therefore phenetic similarities between CAMR and TOGO samples are expected, CAMR linked to IVCO. The West African samples GHAN, TOGO and IVCO were linked as expected, although GHAN is separated from the other two localities by LCAH. However, UGAN is separated from GHAN along the first axis by differences in LCAH, LCAM and FOAR. IVCO does not show pronounced differentiation along the first axis from TOGO and CAMR but separated from all localities along the second axis by ZYGO, CANH, 3M1P, 3MET, 5M2P, CANM and 4M1P (Table 21). No overlapping between confidence circles similar to that in male localities (Fig. 26) is noticeable. Nevertheless, the separation of UGAN from GHAN is distinct.

Table 20

Tadarida thersites females

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 20

FOAR

UGAN	39.23
TOGO	38.49
IVCO	38.39
CAMR	37.86
GHAN	37.82

4MET

UGAN	39.17
TOGO	38.74
IVCO	38.44
CAMR	37.86
GHAN	37.47

5MET

UGAN	27.05
TOGO	26.64
IVCO	26.10
CAMR	25.96
GHAN	25.23

GSLN

TOGO	19.05
UGAN	18.87
IVCO	18.66
CAMR	18.26
GHAN	18.22

CDIN

TOGO	17.55
UGAN	17.45
IVCO	17.26
CAMR	17.04
GHAN	16.80

PALL

UGAN	7.67
TOGO	7.60
IVCO	7.43
CAMR	7.40
GHAN	7.23

BBCS

UGAN	9.76
CAMR	9.52
IVCO	9.50
TOGO	9.47
GHAN	9.35

WBSP

IVCO	1.31
UGAN	1.27
CAMR	1.26
TOGO	1.24
GHAN	1.22

Fig. 26

Bivariate plots of canonical axis 1 against canonical axis II for localities of female T. thersites complex. Locality centroids are enclosed by 95 % confidence circles. A minimum spanning tree connecting locality centroids is shown by broken lines. Contributions of individual characters to the separation of locality centroid are indicated by magnitude and direction of the character vectors, which are scaled relative to the pooled within-group standard deviations. For clarity only those characters with the largest vectors are selected. Refer to text for explanation of abbreviations.

Fig. 26

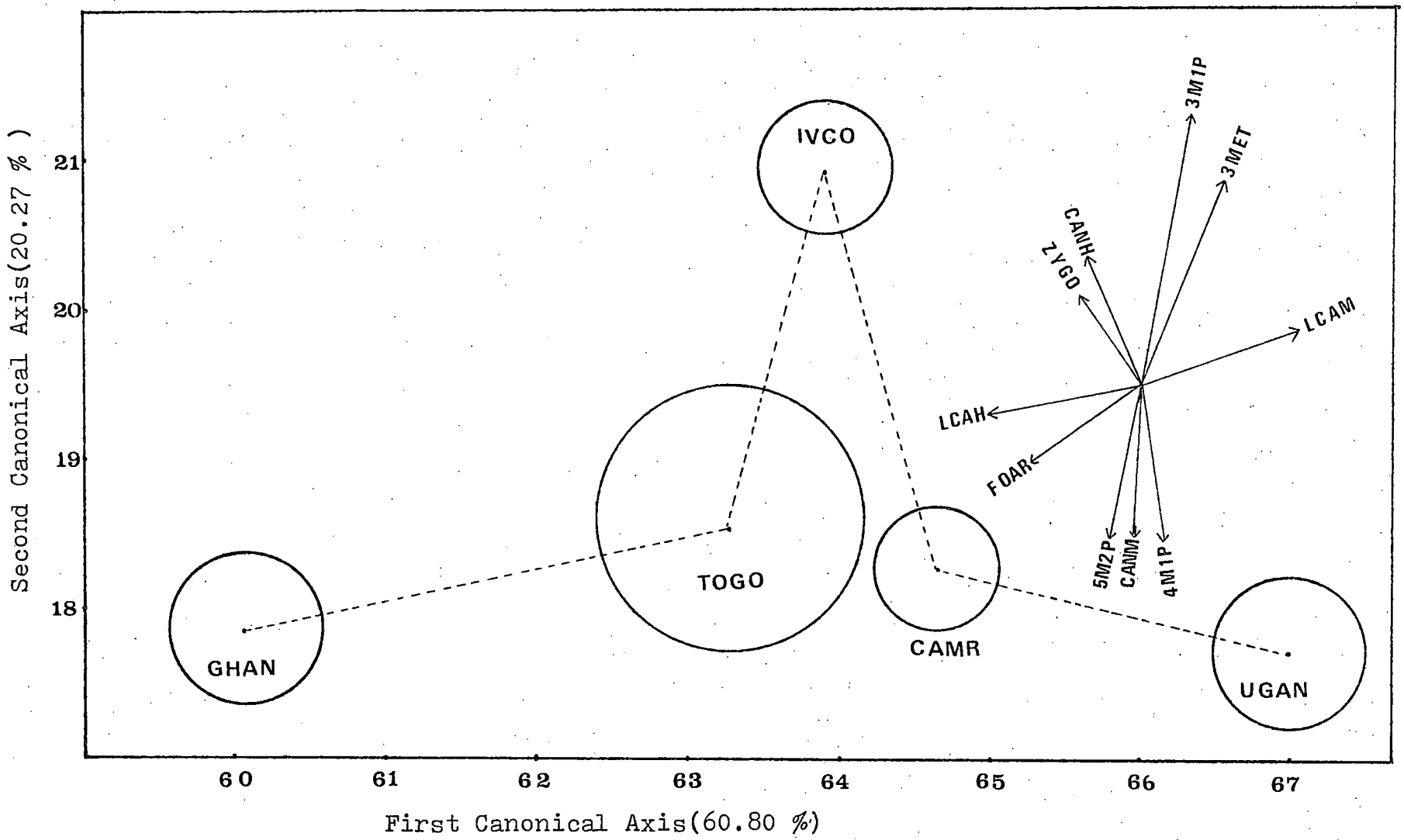

Second Canonical Axis(20.27 %)
21
20
19
18
60
61
62
63
64
65
66
67
First Canonical Axis(60.80 %)
IVCO
TOGO
GHAN
CAMR
UGAN
3M1P
3MET
CANH
ZYGO
LCAM
LCAH
FOAR
5M2P
CANM
4M1P

TABLE 21

Character loadings* on the first two canonical axes of localities of female *T. thersites*. See text for character abbreviations.

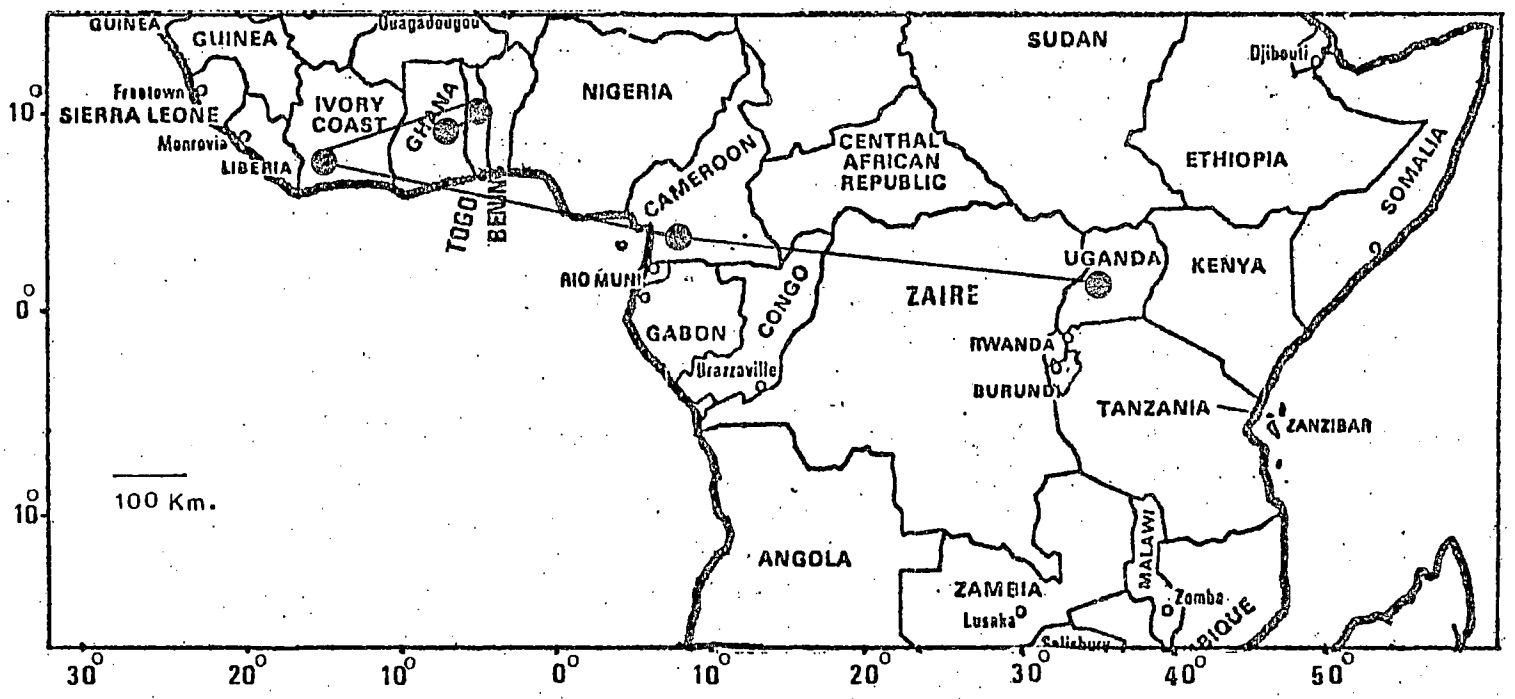
Character	Canonical Axes	
	1	2
FOAR	-0.9250	-0.7235
3MET	0.5448	1.3660
3M1P	0.3266	1.8422
3M2P	-0.5269	0.0436
4MET	-0.1691	-0.4779
4M1P	0.1173	-1.1027
4M2P	-0.1806	-0.2484
5MET	0.8447	-0.4945
5M1P	0.1216	-0.4324
5M2P	-1.1385	-0.2211
GSLN	0.3042	0.1117
CDIN	-0.5769	0.5092
PALL	0.7104	-0.4732
ZYGO	-0.4019	0.6052
MAST	-0.7988	-0.1169
BBCS	0.7231	-0.1927
HBCS	-0.3161	-0.3807
ROWL	0.6632	0.5858
IOWA	-0.4026	-0.1740
POCN	0.4489	-0.8152
M3M3	0.5003	-0.0174
CANM	-1.1861	0.0603
CANC	-0.1474	0.2931
CANH	-0.3821	0.8378
WBSP	0.2803	0.4627
LBSP	-0.7670	-0.9794
CNIL	-0.1518	0.5187
GMLN	0.0182	-0.9957
LCAM	1.4054	0.4527
LCAC	-0.5326	-0.0791
LCAH	-0.1757	-1.3110

*Scaled vectors X pooled within-group standard deviations.

Fig. 27

A minimum spanning tree of the square root of the Mahalanobis distance values superimposed on a map of geographic locations of samples of T. thersites females.

Fig. 27


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
SUDAN
Djibouti
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
ETHIOPIA
SOMALIA
RIO MUNI
UGANDA
KENYA
ZAIRE
GABON
CONGO
Brazzaville
RWANDA
BURUNDI
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
Lusaka
MALAWI
Zomba
Salisbury
MOZAMBIQUE
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

SPUR [T.(X.) spurrelli] -- males

Specimen were represented by three geographic localities as follows:

CANF	4
GHAN	25
CAMR	25

As results of the MANOVA test did not detect any significant differences among samples ($F = 1.22$; df=62 and 42; $P > 0.25$), no further analyses were made.

SPUR [T.(X.) spurrelli] -- females

Samples were as follows:

IVCO	6
GHAN	34
CAMR	33

Analysis of variance detected statistically significant variations among samples in only five characters, namely, FOAR, 4MET 5M2P, PALL and IOWA (Table 22). The CAMR sample is significantly larger than GHAN and IVCO samples in two characters, FOAR and 5M2P. The IVCO sample is significantly smaller in 4MET than in those of the other two localities.

In the MANOVA test samples were significantly different ($F = 3.56$; df=62 and 80; $P < 0.001$), but generalized discriminant analysis produced only one significant root that explains 86.96 per cent of the total variation among locali-

ties. It was therefore only possible to show dispersion of localities along the first canonical axis. Individual scores are plotted in a histogram given in Fig. 28. An overlap between samples from GHAN and IVCO indicates phenetic similarities between the two localities. Samples from CAMR are clearly separated from GHAN and IVCO. However, MST superimposed on the map of geographic locations connected IVCO with GHAN and GHAN with CAMR, and therefore corresponded with geographical distances (Fig. 29).

Table 22

Tadarida spurrelli females

Results of analysis of variance and SS-STP procedure. Maximally nonsignificant subsets are shown by vertical lines. Character means are ranked in decreasing order. Refer to text for explanation of abbreviations.

Table 22

FOAR

CAMR	28.43
GHAN	27.63
IVCO	27.25

4MET

CAMR	27.99
GHAN	27.95
IVCO	26.57

5M2P

CAMR	2.58
GHAN	2.36
IVCO	2.12

PALL

GHAN	6.21
IVCO	6.06
CAMR	5.92

IOWA

GHAN	4.54
IVCO	4.49
CAMR	4.00

Fig. 28

T. spurrelli female samples projected on the first canonical axis. Stippled area represents Ivory Coast sample. Refer to text for explanation abbreviations.

Fig. 28

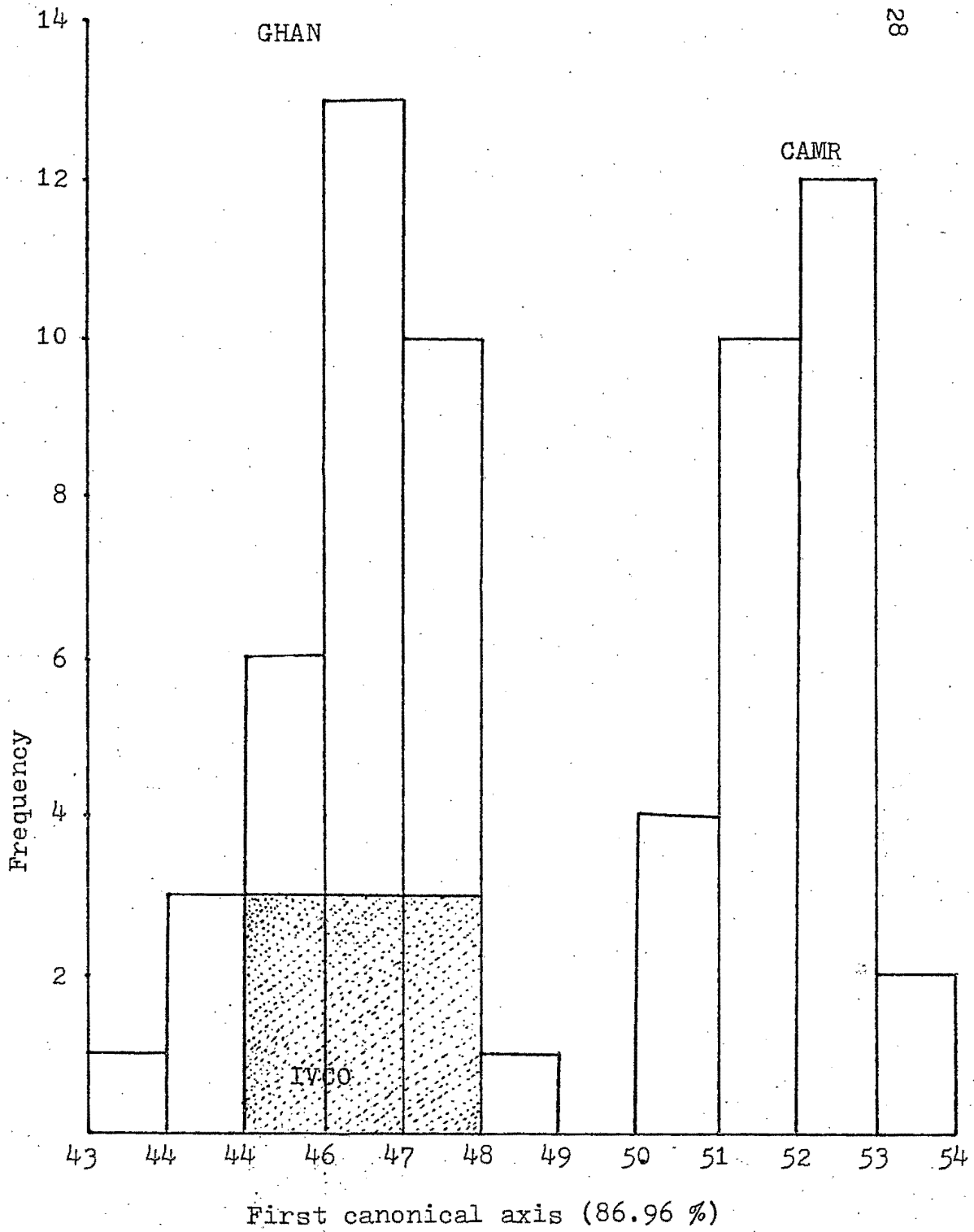
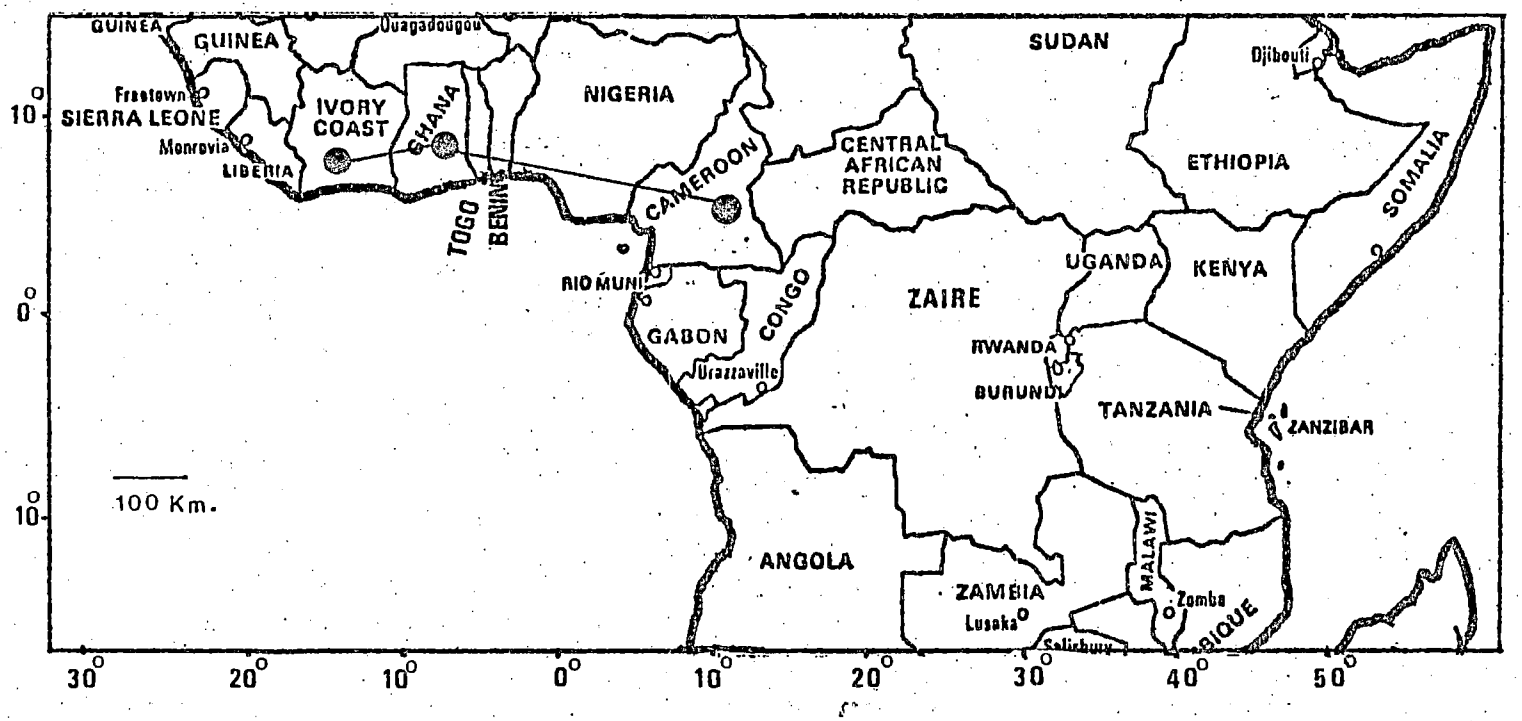

GHAN
CAMR
IVCO
Frequency
14
12
10
8
6
4
2
43
44
44
46
47
48
49
50
51
52
53
54
First canonical axis (86.96 %)

Fig. 29

A minimum spanning tree of the square root of the Mahalanobis' distance values superimposed on a map of geographic locations of T. spurrelli females.

Fig. 29


GUINEA
GUINEA
Ouagadougou
Freetown
SIERRA LEONE
IVORY COAST
GHANA
NIGERIA
SUDAN
Djibouti
Monrovia
LIBERIA
TOGO
BENIN
CAMEROON
CENTRAL AFRICAN REPUBLIC
ETHIOPIA
SOMALIA
RIO MUNI
GABON
CONGO
ZAIRE
UGANDA
KENYA
RWANDA
BURUNDI
Brazzaville
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
Lusaka
MALAWI
Zomba
Salisbury
MOZAMBIQUE
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

Interspecific Relationships

The result of PCA/MDSCALE showed that T. "subleonis" occupies an intermediate position between T.(X.) nanula and T.(X.) leonis. This relation was not only confirmed by MST and subsets procedures but also corroborated by cluster analysis in average taxonomic distance phenograms (Figs. 14, 15) and to a lesser extent, in correlation coefficients phenograms (Figs. 12, 13). Moreover, T. "subleonis" is sympatric with nanula and leonis in Ghana and the Cameroun. It is therefore warranted to examine in detail the relationship of T. "subleonis" to nanula and leonis. In this respect, a discriminant function analysis was used as an a posteriori procedure to eludicate differences among these three taxa. The discriminant analysis procedure in the SPSS was followed. Males and females were treated separately.

Tadarida nanula, T. "subleonis", T. leonis -- males

The number of males used in this study were as follows:

NANU	(T. nanula)	29
SBLN	(T. "subleonis")	14
LEON	(T. leonis)	45

Two significant discriminant functions ($P < 0.001$) were generated that explained 87.38 and 12.62 per cent of the variation among taxa (total of 100%). The number of specimens correctly classified in each taxon was 100 per

cent. Results are given in Fig. 30 where discriminant function coefficients that maximally separate the groups are represented by scaled vectors that show the magnitude and direction along which character differences occurred. SBLN is separated from NANU by HBCS, 5M1P and CDIN. Furthermore, SBLN is also separated from LEON by LCAH, CNIL, 3M1P and GSLN. Vectors also show that LEON is separated from NANU by 3M1P, GSLN, FOAR and HBCS.

T. nanula, T. "subleonis" and T. leonis -- females

Females were represented as follows:

NANU	67
SBLN	23
LEON	74

Discriminant function analysis was performed (as above) and 100 per cent of specimens were correctly identified in each taxon. Two significant discriminant functions were produced that explained 89.32 and 10.86 per cent of the variation (total of 100%). Results are given in Fig. 31. SBLN is separated from both NANU and LEON by LCAC, GSLN, CDIL, CNIL, LCAM and WBSP.

It is therefore concluded that T. "subleonis", although belonging to the Xiphonycteris groups, is distinct in view of morphological differences and sympatry with T. nanula and T. leonis.

Fig. 30

Dispersion of scores of Tadarida nanula, T."subleonis" and T. leonis males on the first and second discriminant functions that account for 100 % of the total variation among species. Polygons enclose all bats in each group. For clarity only those characters with the largest vectors are depicted. Vectors are represented by arrows drawn against a scale separate from that of species scores.

Fig.30

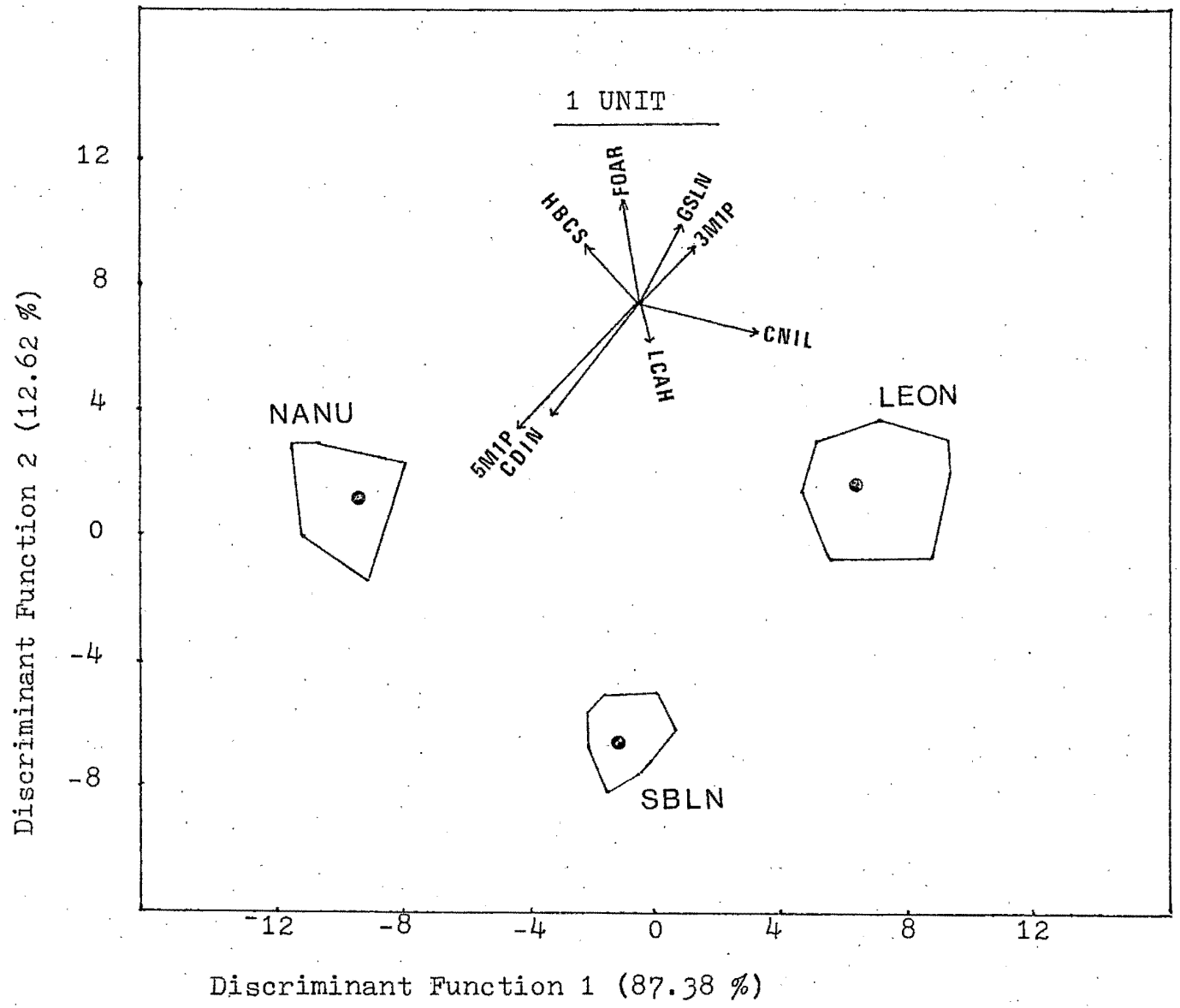
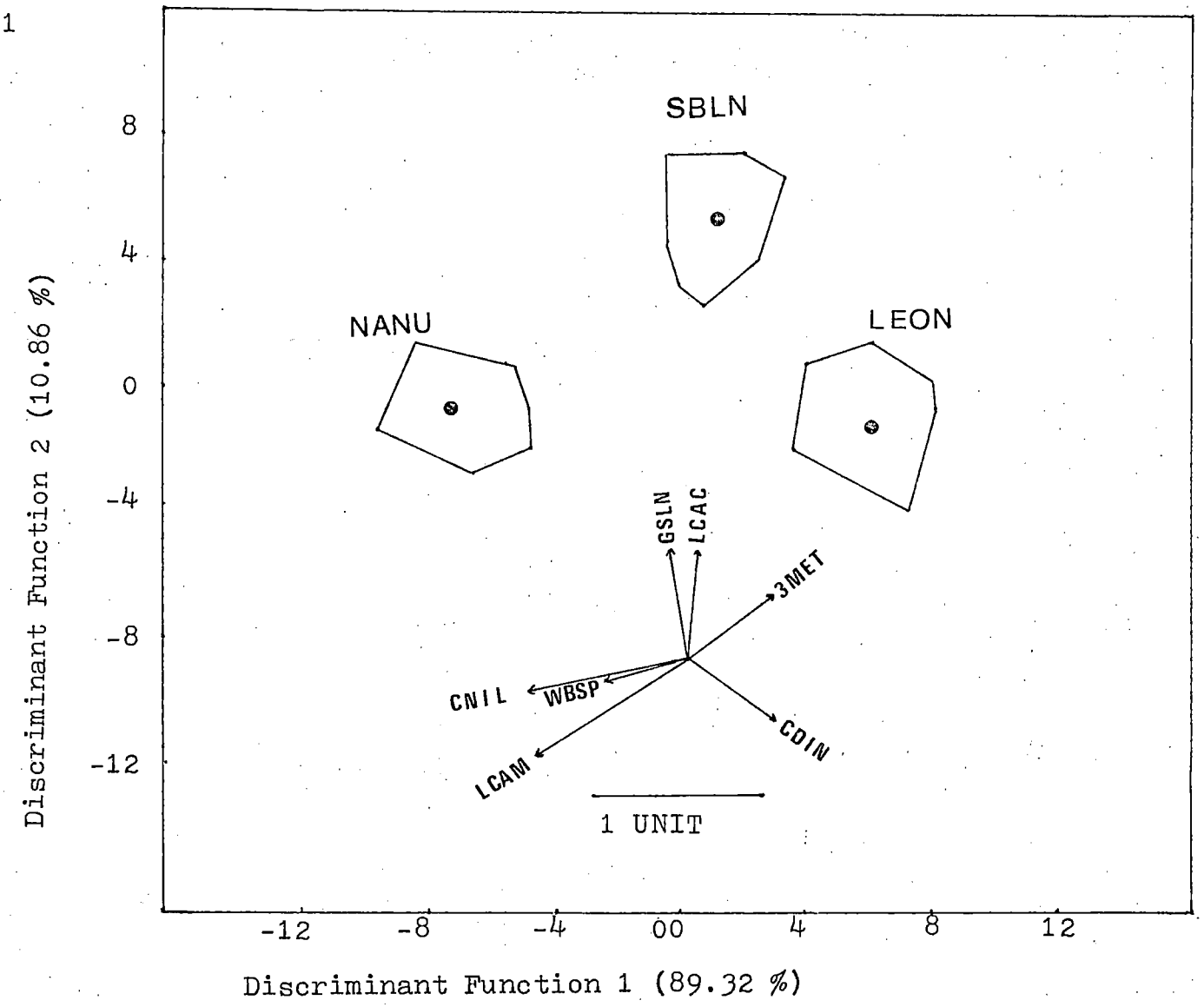

1 UNIT
FOAR
GSLN
3M1P
HBCS
CNIL
LCAH
5M1P
CDIN
NANU
LEON
SBLN
12
8
4
0
-4
-8
-12
-8
-4
0
4
8
12
Discriminant Function 2 (12.62 %)
Discriminant Function 1 (87.38 %)

Figure 31

Dispersion scores of Tadarida nanula, T. "subleonis" and T. leonis females on the first and second discriminant functions that account for 100 % of the total variations among species. Polygons enclose all bats in each group. For clarity only those characters with the largest vectors are depicted. Vectors are represented by arrows drawn against a scale separate from that of species scores.

Fig. 31


SBLN
NANU
LEON
GSLN
LCAC
3MET
CNIL
WBSP
COIN
LCAM
1 UNIT
8
4
0
-4
-8
-12
-12
-8
-4
00
4
8
12
Discriminant Function 2 (10.86 %)
Discriminant Function 1 (89.32 %)

Morphological Comparison of *T. leonis*, *T. thersites* and *T. brachyptera*

To settle nomenclatorial problems related to *T. leonis*, *T. thersites* and *T. brachyptera*, a comparison of measurements given by Peters (1852) in his original description of *T. brachyptera* with measurements of the other two taxa was warranted (Table 23). Although information about methods employed in measuring the holotype is not available, *T. brachyptera* appears to be more similar to *T. leonis* than to *T. thersites*.

Table 23

A comparison of T. brachyptera as given by Peters (1852) with means of six T. leonis males and nine T. thersites males from the Budongo Forest, Uganda.

Character	T. leonis		T. brachyptera	T. thersites.	
	$\bar{X}$	Range		$\bar{X}$	Range
FOAR	38.2	37.7-39.1	37	39.6	37.20-41.50
3MET	40.1	38.3-40.7	36.5	40.8	39.60-42.70
3M1P	15.5	14.6-16.2	15.0	16.6	15.70-17.30
3M2P	14.9	13.1-15.8	14.0	15.7	14.90-16.00
4MET	38.3	36.4-39.1	35.0	39.3	37.50-41.20
4M1P	12.2	11.4-13.1	12.0	13.7	13.60-14.70
4M2P	9.0	8.40-9.60	8.5	11.3	9.80-12.10
5MET	25.8	25-26.70	22.0	27.18	25.60-28.0
5M1P	10.5	9.60-10.5	9.0	10.64	10.20-10.90
5M2P	3.6	3.30-4.00	3.25	3.29	2.60-3.60
Tibia	12	11-13	12.00	14,00	13.00-15.00
GSLN	19.8	18.7-20.15	21.40	19.49	18.45-19.80

$\bar{X}$: means. Refer to text for explanation of abbreviations.

Phenetic Similarities Among *Xiphonycteris*-*Mops* OTU's

From the foregoing study only five species in the subgenus *Xiphonycteris* are regarded as valid: *T.(X.) nanula*, which includes NANU and CALB; *T.(X.) spurrelli*; *T.(X.) leonis* which includes LEON, BRAC and OCHR; *T.(X.) thersites* which includes THER and OCCP; and *T.* "subleonis".

Because the aim of this study is to approach the systematic problem without an *a priori* judgement, valid taxa in the recently defined subgenus *Xiphonycteris* (Koopman, 1975) were compared in a phenetic study with selected taxa from the subgenus *Mops* in what I tentatively designate as the Xipho-Mops complex. Taxa were selected from the subgenus *Mops* using the following criteria:

1. they are all African taxa,
2. their systematic status is presently accepted, and
3. they represent a wide range in shape and size.

The species selected were: *T.(M.) demonstrator* (DEMO), *T.(M.) condylura* (COND), *T.(M.) congica* (CONG), *T.(M.) trevori* (TREV), *T.(M.) midas* (MIDA). Relevant multivariate procedures in the NT-SYS package were used to elucidate phenetic similarities among taxa in the Xipho-Mops complex.

Cluster Analysis

Data were standardized to have a mean of zero and a unit variance. Correlation coefficients and average taxo-

nomic distances were computed for 10 OTU's and results are summarized separately in phenograms for males and females.

Phenogram of Correlation Coefficients - Males

Four hierarchical groupings were produced for male OTU's by the UPGMA method:

1. NANU and SPUR
2. THER and COND
3. LEON, SBLN and TREV
4. DEMO, MIDA and CONG

Results of clustering are illustrated in Fig. 32. The cophenetic correlation coefficient for this phenogram was 0.768.

Females were also clustered into four hierarchical groupings but with different arrangements:

1. NANU with SPUR
2. THER, COND and DEMO
3. LEON and SBLN
4. TREV, CONG and MIDA

Results are shown in Fig. 33. With a cophenetic correlation coefficient of 0.821, this phenogram represents a better summary of the information originally contained in the matrix of correlation coefficient than does the phenogram of males. In both phenograms, SBLN clustered with LEON, indicating a similarity in shape between the two species.

Phenograms of Average Taxonomic Distance

Only three hierarchical groupings were produced for male OTU's by the UPGMA method:

1. NANU, SPUR and SBLN
2. LEON, THER, DEMO and COND
3. TREV, CONG and MIDA

Results are shown in Fig. 34. The cophenetic correlation was o.797. This phenogram which orders OTU's by size, explains the clustering of SBLN with the NANU group because of the similarity in size. In a more logical arrangement LEON, THER, DEMO and COND group together, and such OTU's that represent members with large sizes as TREV, CONG and MIDA group into a separate cluster.

Similar groupings were produced by the phenogram of average taxonomic distances for females:

1. NANU, SPUR and SBLN
2. LEON, THER, DEMO and COND
3. TREV, CONG and MIDA

Results are shown in Fig. 35. Low values for taxonomic distances between groups were considered to indicate similarities among OTU's. The cophenetic correlation coefficient was 0.820. The male and female phenograms are identical and represent a more consistent relationship between OTU's than do phenograms of correlation coefficients.

Principal Component Analysis/Multidimensional Scaling

Male and female OTU's of the Xipho-Mops complex were subjected to PCA and MDSCALE and results are shown in Figs. 36 (males) and 37 (females). MST and subsets were superimposed on the resulting 3-D diagram to illustrate the possible distortions in relationships among OTU's as well as their similarities.

PCA was first performed on the matrix of character correlations, and three factors that explained 90.02, 4.92 and 2.44 per cent of character variations among OTU's (total of 98.02%) were generated.

Character loadings shown in Table 24 were used to interpret the 3-D diagram (Fig. 36) of the PCA/MDSCALE configuration. All characters loaded heavily and positively on the first principal component with the exception of WBSP and LBSP, indicating that OTU's are separated along the first factor, predominantly on size relationships. On the second principal component WBSP loaded heavily in an inverse relationship with LBSP, which loaded negatively. 4M2P loaded positively and also contributed in the separation of THER and LEON, COND and DEMO, and CONG and MIDA along the second factor. Along the third factor LBSP, PALL, and 4M2P are important characters to separate DEMO and MIDA from other OTU's. The PCA/MDSCALE has a stress of 0.001 and a correlation of 0.988, indicating no significant loss of information in the original

similarity matrix. The MST superimposed on the 3-D diagram linked morphologically similar OTU's. Subsets routine grouped NANU and SPUR in one subset and also added to this subset SBLN in a larger subset. The subsets procedure also grouped THER and LEON, TREV and CONG into two subsets with only DEMO, COND and MIDA not grouped into any subsets.

When PCA was performed on the matrix of character correlations for female OTU's, three factors that explained 92.66, 5.18 and 1.00 per cent of character variations among OTU's (total of 98.84%) were produced.

Results of the joint PCA/MDSCALE ordination are shown in Fig. 37. Character loadings shown in Table 25 are used to interpret the placement of OTU's onto the 3-D configuration. It is clear that female OTU's are in a configuration similar to that of male OTU's and also connected by MST and grouped by subsets procedures in identical grouping. However, CONG is separated from other OTU's by POCN along the third axis. MDSCALE ordination produced a perfect stress of 0.0 and a correlation of 0.999.

In both diagrams for male and female OTU's (Figs. 36, 37) it is apparent that DEMO and COND are not only related phenetically to the Xiphonycteris group but also occupy an intermediate position between the species grouped in Xiphonycteris and the larger size taxa of the Mops group.

Figure 32

Phenogram of correlation coefficients of males of the Xipho-Mops complex. The cophenetic correlation coefficient is 0.768. Refer to text for explanation of abbreviations.

Fig . 32

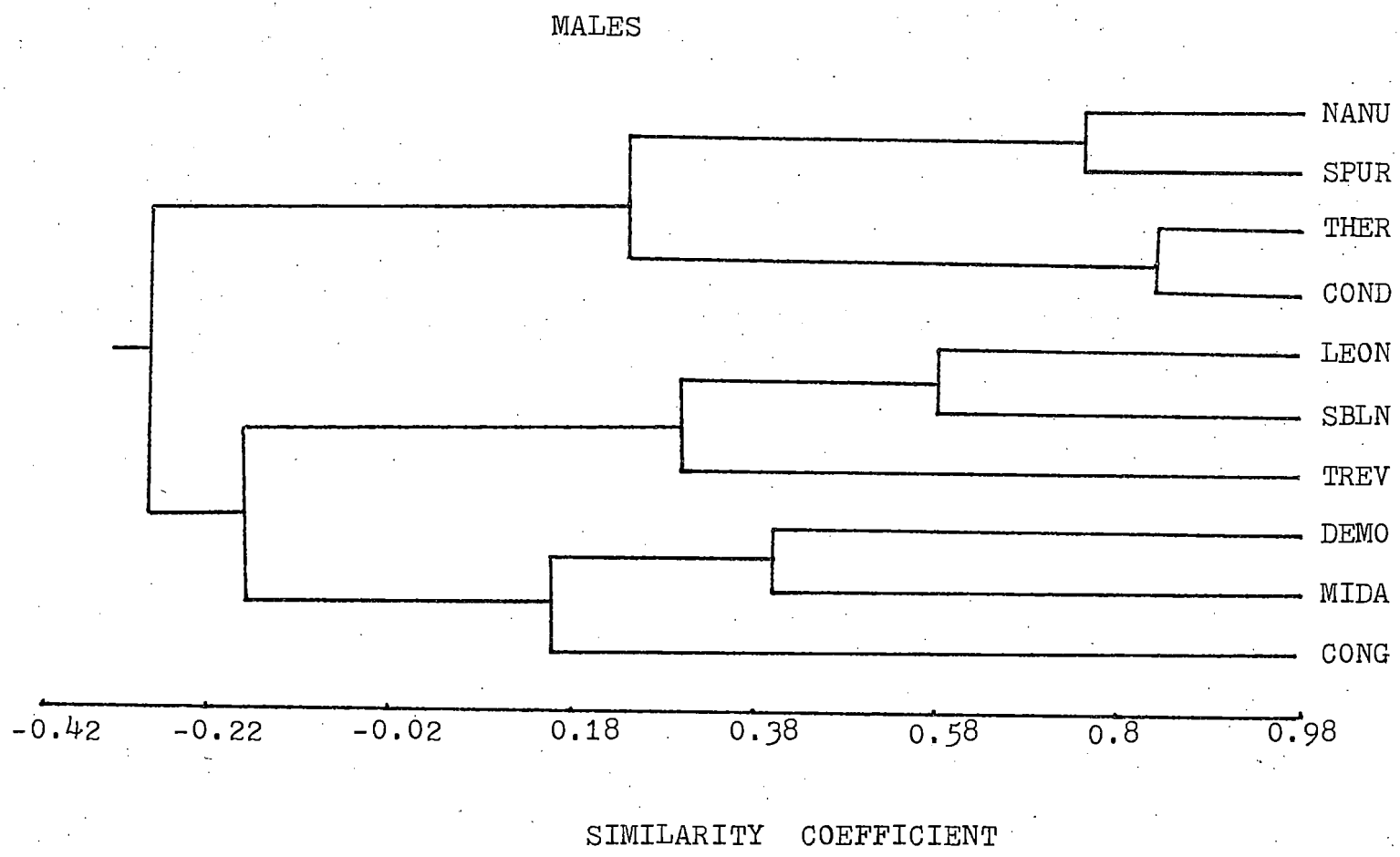

MALES
NANU
SPUR
THER
COND
LEON
SBLN
TREV
DEMO
MIDA
CONG
-0.42
-0.22
-0.02
0.18
0.38
0.58
0.8
0.98
SIMILARITY COEFFICIENT

Fig. 33

Phenogram of correlation coefficients of females of the Xipho-Mops complex. The cophenetic correlation coefficient is 0.821. Refer to text for explanation of abbreviations.

Fig. 33

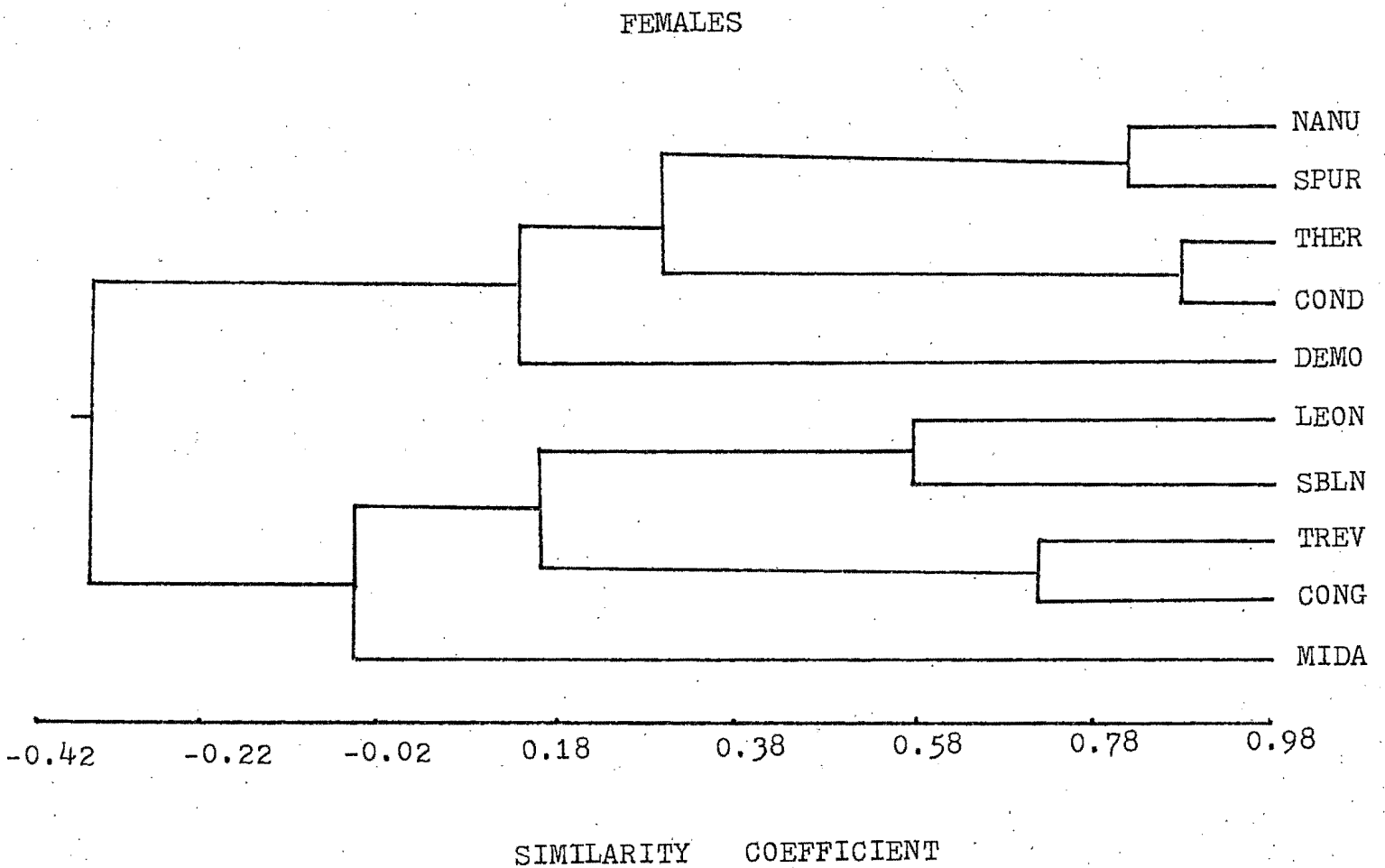

FEMALES
NANU
SPUR
THER
COND
DEMO
LEON
SBLN
TREV
CONG
MIDA
-0.42
-0.22
-0.02
0.18
0.38
0.58
0.78
0.98
SIMILARITY COEFFICIENT

Fig. 34

Phenogram of average taxonomic distance of males of the Xipho-Mops complex. The cophenetic correlation coefficient is 0.797. Refer to test for explanation of abbreviations.

Fig. 34

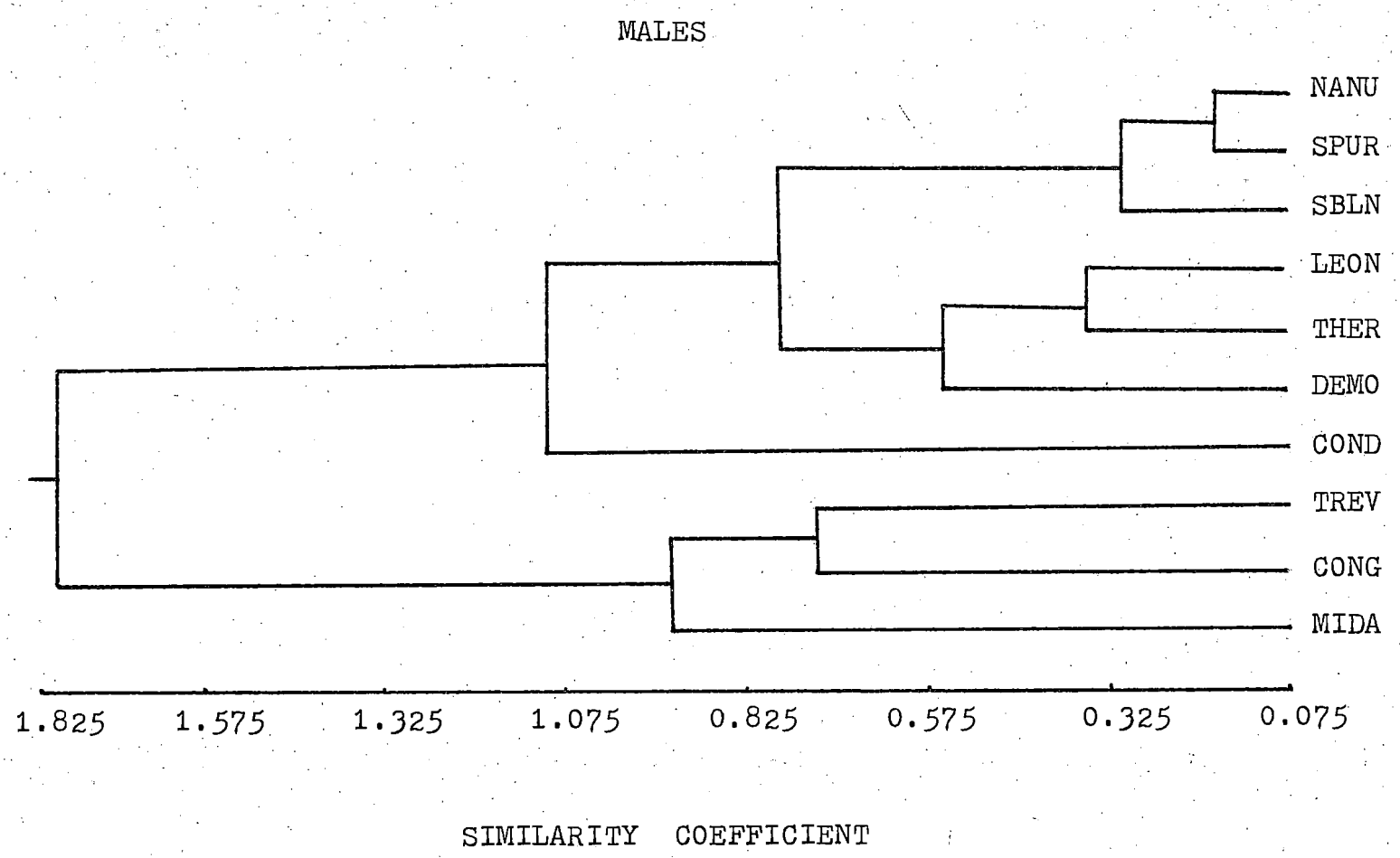

MALES
NANU
SPUR
SBLN
LEON
THER
DEMO
COND
TREV
CONG
MIDA
1.825
1.575
1.325
1.075
0.825
0.575
0.325
0.075
SIMILARITY COEFFICIENT

Fig. 35

Phenogram of average taxonomic distance of females of the Xipho-Mops complex. The cophenetic correlation coefficient is 0.820. Refer to text for explanation of abbreviations.

Fig. 35

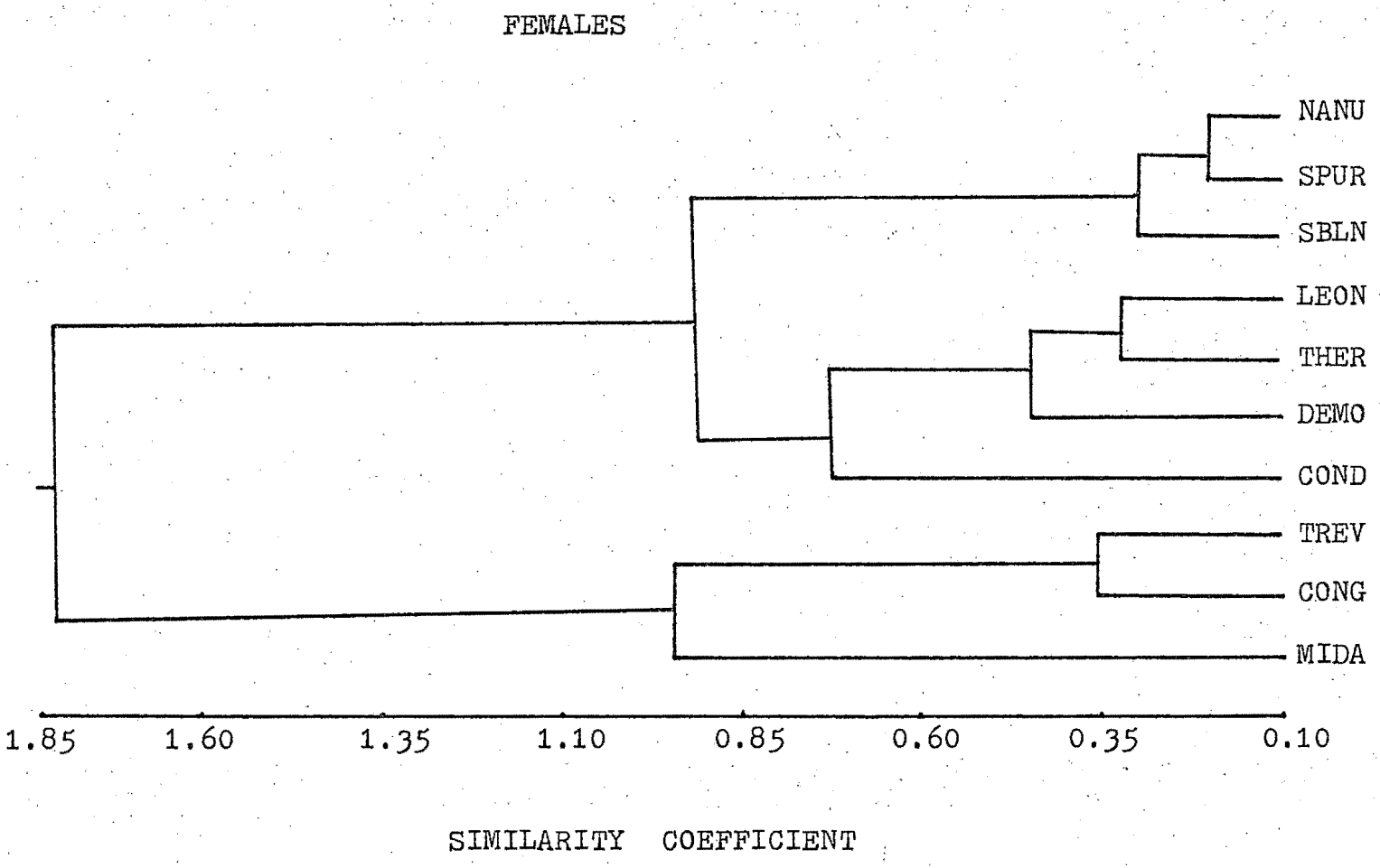
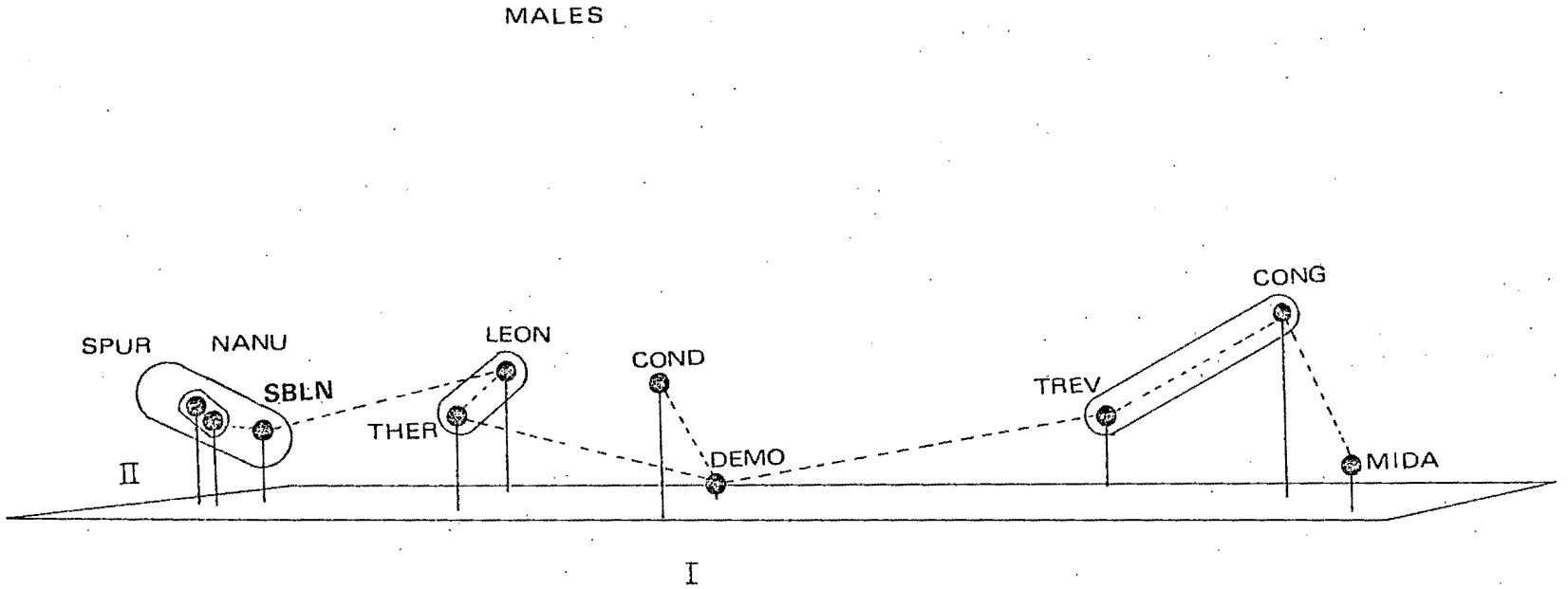

FEMALES
NANU
SPUR
SBLN
LEON
THER
DEMO
COND
TREV
CONG
MIDA
1.85
1.60
1.35
1.10
0.85
0.60
0.35
0.10
SIMILARITY COEFFICIENT

Fig. 36

Three-dimensional configuration of male OTU's of Xipho-Mops complex using the PCA/MDSCALE procedure. Component I and II are shown whereas component III is represented by the height of the projections. Stress is denoted by s and the matrix correlation by r_{dd^*}. MST is indicated by broken lines joining phenetically-similar OTU's. Subsets are enclosed in solid lines. Refer to text for explanation of abbreviations.

Fig. 36



$r_{dd}^{*} = 0.988$

$s = 0.001$

TABLE 24

Character loadings on the first three principal components computed from the character correlation of ten male Xipho-Mops OTU,s. See text for character abbreviations.

CHARACTER	COMPONENTS		
	1	2	3
FOAR	0.997	-0.043	-0.022
3MET	0.997	-0.023	-0.012
3M1P	0.991	0.045	-0.025
3M2P	0.988	0.106	-0.104
4MET	0.007	-0.008	-0.006
4M1P	0.988	0.034	-0.009
4M2P	0.800	0.490	-0.310
5MET	0.984	0.105	-0.108
5M1P	0.994	0.024	-0.000
5M2P	0.955	0.003	-0.241
GSLN	0.997	-0.033	0.033
CDIN	0.993	-0.051	0.065
PALL	0.902	-0.063	0.400
ZYGO	0.993	-0.014	0.046
MAST	0.989	-0.103	-0.054
BBCS	0.991	-0.069	0.018
HBCS	0.968	-0.007	-0.095
ROWL	0.994	-0.069	0.026
IOWA	0.981	-0.059	-0.100
POCN	0.930	-0.040	-0.133
M3M3	0.988	-0.025	0.002
CANM	0.984	-0.085	0.039
CANC	0.991	0.024	0.103
CANH	0.984	0.001	0.112
WBSP	0.292	0.938	-0.098
LBSP	0.680	-0.560	-0.453
CNIL	0.985	0.016	0.158
GMLN	0.990	-0.029	0.124
LCAM	0.981	-0.044	0.110
LCAC	0.987	-0.011	0.021
LCAH	0.928	0.131	0.277

Fig. 37

Three-dimensional configuration of female OTU's of Xipho-Mops complex using the PCA/MDSCALE procedure. Component I and II are shown whereas component III is represented by the height of the projections. Stress is denoted by s and the matrix correlation by r_{dd*}. MST is indicated by broken lines joining phenetically-similar OTU's. Subsets are enclosed in solid lines. Refer to text for explanation of abbreviations.

Fig. 37

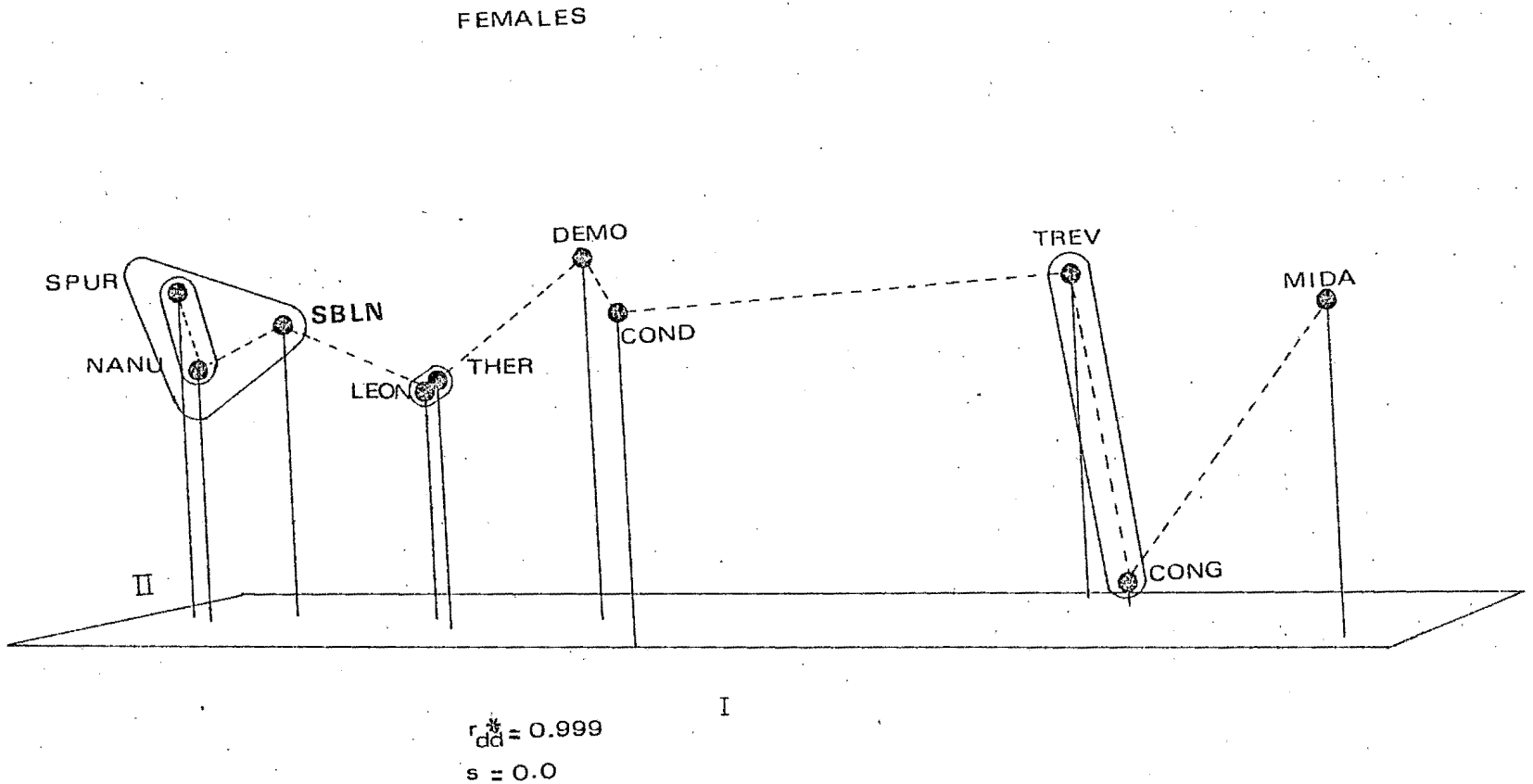

FEMALES
SPUR
SBLN
NANU
LEON
THER
DEMO
COND
TREV
MIDA
CONG
II
I
r_{dd}^{*} = 0.999
s = 0.0

TABLE 25

Character loadings on the first three principal components computed from the character correlation matrix of ten female Xipho-Mops OTU,s. See text for character abbreviations.

CHARACTER	COMPONENTS		
	1	2	3
FOAR	0.998	-0.006	-0.006
3MET	0.997	-0.013	-0.013
3M1P	0.993	0.037	-0.106
3M2P	0.988	0.131	-0.050
4MET	0.998	0.002	-0.008
4M1P	0.987	0.031	-0.133
4M2P	0.796	0.565	-0.012
5MET	0.988	0.128	-0.050
5M1P	0.997	-0.004	-0.004
5M2P	0.953	0.148	0.154
GSLN	0.996	-0.074	0.013
CDIN	0.993	-0.077	0.042
PALL	0.999	0.003	0.037
ZYGO	0.995	-0.061	0.052
MAST	0.990	-0.096	-0.042
BBCS	0.991	-0.079	-0.099
HECS	0.986	0.013	-0.059
ROWL	0.997	-0.025	-0.009
IOWA	0.980	0.072	0.098
POCN	0.926	-0.048	-0.360
M3M3	0.990	-0.018	0.132
CANM	0.988	-0.074	0.125
CANC	0.998	-0.042	0.015
CANH	0.986	-0.101	-0.076
WBSP	0.277	0.957	0.001
LBSP	0.827	-0.483	0.059
CNIL	0.992	-0.095	-0.026
GMLN	0.993	-0.088	-0.022
LCAM	0.990	-0.052	0.121
LCAC	0.995	0.027	0.038
LCAH	0.978	0.049	0.179

DISCUSSION

Sexual Dimorphism

Sexual dimorphism in size and colour or pattern is well known in vertebrates. Many examples are available for mammals; Microtus pennsylvanicus (Guilday, 1951), Colobus badius (Cave and Steel, 1964; Kingdon, 1971), Lutra canadensis (Van Zyll de Jong, 1972), Elephantulus sp. (Rautenbach and Schlitter, 1977).

Sexually dimorphic characters in Chiroptera have been recorded by Phillips (1927) and Brosset (1962), who confirmed the existence of sexual dichromatism in some emballonurid and pteropodid bats. Allen (1937) also recorded contrasting colour differences in Noctilio leporinus (Noctilionidae). All adult males examined by Allen were brightly coloured, whereas females were paler. Peterson (1966) stated that male Lasiurus borealis (Vespertilionidae) are bright chestnut-red in colour whereas females are much duller and paler than males.

Examples of secondary, nonmetric-sexual differences in male bats are summarized by Kingdon (1974: 115) as follows: shoulder pocket (Epmophorus sp.), gular pouch (Taphozous sp.), axillary tuft in "armpit" (Rhinolophus landeri), forehead pocket (Hipposideros commersoni), muzzle and other facial glands (Vaspertilionidae), anal sacs (Tadarida cistura). Also a chest gland in Phyllostomus discolor (Phyllostomatidae) is functional in males but vestigial in females (Valdivieso and Tamsitt, 1965).

The study of sexual dimorphism in bats has become a prerequisite for phenetic studies. Secondary sexual differences between males and females are sometimes so pronounced that to pool measurements of males and females would obscure important biological information. Peterson (1965) showed that the two species of Ametrida (A. centurio and A. minor) were in fact the same species, with the smaller male incorrectly described as A. minor. Eumops amazonicus was described as a new species by Handley (1955). Later, Gardiner et al. (1970) synonymized E. amazonicus with E. hansae after showing that E. amazonicus was in fact the female of E. hansae described by Sanborn in 1932. This conclusion was confirmed by Eger (1977).

The size of the anterior lower premolar found to be dimorphic in males and females of T. aloysiisabaudiae (Peterson, 1969) and in T. spurrelli (De Vree, 1969) was later confirmed by Turner (1970). In males of these two species, the first lower premolar is larger at the base than the second lower premolar, whereas in females, the first lower premolar is smaller than the second. These sex-related differences in premolar size characterize all species in the Xipho-Mops complex that I examined.

Comprehensive studies of sexual dimorphism in bats include those by Herreid (1959), Eger (1977) and Turner (1970), who devoted his study to an investigation of sexual dimorphism in cranial characters of 29 species of molossid

bats. Turner found that sexual dimorphism was not related to geographic variation, but suggested that evolutionarily advanced species tended to be more sexually dimorphic, with some exceptions in smaller species.

In this study I found that T. spurrelli was the smallest species but showed the strongest sexual dimorphism, whereas T. midas the largest species, was the least dimorphic (Fig. 11). However, there is no evidence that T. spurrelli is evolutionarily advanced compared to T. midas or any other less dimorphic species.

In the present study, sexual dimorphism was not just related to size. Discriminant function analyses showed that, although some characters were not significantly different in t-tests, they contributed to the separation of the sexes along the discriminant axis. This discrepancy may be explained by the covariation of all characters in discriminant analysis being tested simultaneiously, whereas in t-tests only two characters are tested at a time. However, discriminant function analysis, with its positive and negative loadings, shows that subtle shape differences are involved that may not be detected by t-tests (Power and Tamsitt, 1973). Such characters in the above analyses included the second phalanx of the fourth metacarpal in T. nanula, width of the septum between basisphenoid pits in T. leonis and the third metacarpal bone in T. "subleonis".

There were no dimorphic colour patterns in any of the species examined. Colour variations exhibited by male and female T. nanula and T. brachyptera from the Budongo Forest, Uganda, were not related to sexual dimorphism, as both males and females showed both bright and pale pelage colours.

Because the social behaviour of bats has not been studied in depth, any inference regarding selective advantages of sexual dimorphism would be speculative. Size differences, for example, may help to segregate the sexes ecologically and thus reduce intraspecific competition. Males may feed on larger insects than do females and therefore have large jaws and teeth. Furthermore, perhaps larger size of wings in males indicate longer distances travelled in search of food, with females foraging near their roost sites, or maybe larger bodies require larger wings.

However, the mere knowledge that the sexes are significantly different is valuable in any phenetic or phyletic study. It was therefore essential to treat males and females separately in this study.

Phenetic Similarities Among Xiphonycteris OTU's

All multivariate procedures showed that three distinct groupings within Xiphonycteris exist: the T. nanula

complex which includes calabarensis; the T. leonis comlex, which includes ochraceus and brachyptera; and the T. thersites complex which includes occipitalis. T. spurrelli associates with the T. nanula group. But T. "subleonis" links with the T. leonis complex in phenograms of correlation coefficients and with T. nanula group in phenograms of taxonomic distances. This is because phenograms of correlation coefficients group taxa according to their shape similarities, whereas phenograms of taxonomic distances order them by size (Sokal and Rohlf, 1962).

Members of T. "subleonis" are similar to T. leonis, especially in the shape of the basisphenoid pits and the degree of reduction in the third commissure on M^3. This similarity to T. leonis explains the tentative name T. "subleonis" given to the specimens from Cameroun and Ghana in the collection of the Department of Mammalogy of the ROM by Dr. R. L. Peterson and the name T. leonis given to similar specimens in the AMNH. However, in size, T. "subleonis" associates with T. nanula, especially in some cranial measurements, whereas wing measurements place T. "subleonis" in an intermediate position between T. nanula and T. leonis, especially in PCA/MDSCALE analyses (Figs. 16, 17).

The association of T. calabarensis and T. nanula is expected because of lack of apparent distinguishing morphologic characters between the two taxa. When Hayman

(1940: 678) designated T. calabarensis a new species, he indicated that "the first and second lower premolars appear subequal viewed from the outside, but in crown area the first is as half as large again as the second, in which point this bat differs notably from Mops nanulus J. A. Allen, of approximately similar dimension". When I examined the male holotype of T. nanula (AMNH 48864) I noticed that the first and second lower premolars were eroded and, therefore, appear to be equal in size. Moreover, when I examined other specimens of T. nanula and T. calabarensis I detected no obvious differences between them.

On the other hand, T. spurrelli, though distinct from T. nanula, is phenetically related to it. In size T. spurrelli is slightly smaller than T. nanula and may be distinguished by the peculiar shape of the upper and lower canines, which bear enormous cingula. Moreover, in T. spurrelli the upper incisors are on the same plane as the canines, where in T. nanula they occupy the most anterior edge of the premaxilla. Besides, in T. spurrelli the upper incisors are widely separated at the base, and the cutting angles are apically sharper than in T. nanula (Fig. 38). However, the two species are sympatric throughout a large part of their range.

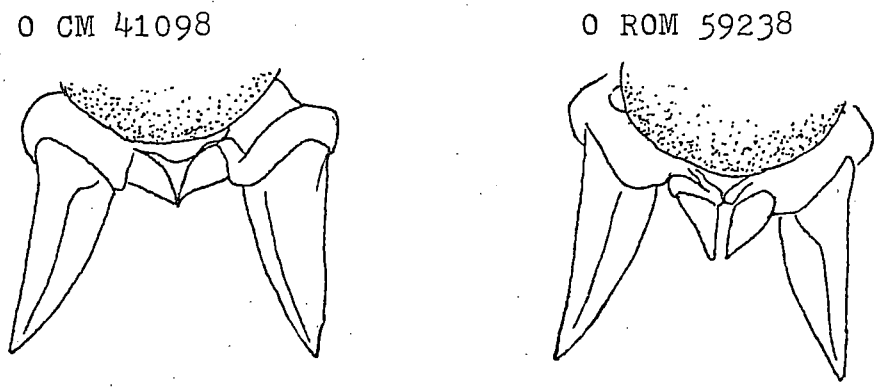
Results of ordination routines that grouped T. leonis, T. brachyptera and T. ochraceus in one complex are not unexpected. T. leonis and T. brachyptera are differentiated mainly by differences in skull lengths, whereas T. ochraceus is differentiated from T. leonis and T. brachyptera by the ventral pelage colour, which is Ochraceous-Orange in T. ochraceus and much paler in the other two species.

Ordination procedures consistently grouped T. thersites and T. occipitalis. The main diagnostic character used by Allen (1917) to designate T. occipitalis as a new species different from T. thersites is the shape of the premaxilla, which he thought to be closed in T. occipitalis and open in T. thersites. It was therefore necessary to use results of ordination procedures to analyse geographic variation in all groups mentioned.

Fig. 38

The position of upper incisors and the direction of cutting angles in T. spurrelli and T. nanula.

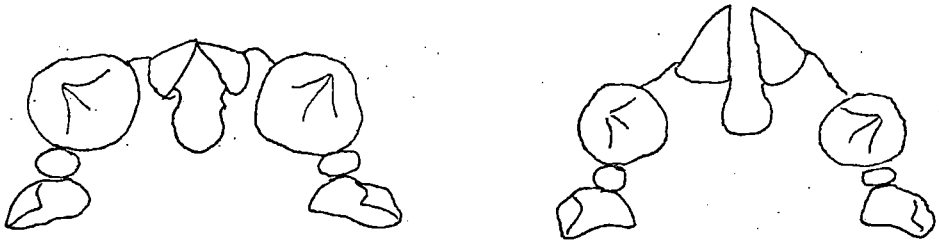
Fig. 38



T. spurrelli T. nanula

Anterior View

2 mm



T. spurrelli T. nanula

Ventral View

Geographic Variation

Any study of geographic variation within populations of any species requires sufficiently large samples that are random with respect to locality, age, sex and environmental data. Normally, museum collections are only fragments of natural samples and are often too incomplete to allow for reasonable inferences to be drawn from the examination of small samples. Moreover, in discriminant function analysis the assumption is made that the convariance matrices are roughly the same size and the variances within-samples are homogeneous, a condition sometimes difficult to satisfy when dealing with small samples. However, canonical variate analysis has the reputation of being reliable, even when assumptions of multivariate normality and homogeneity of within-sample variance-covariance matrices are not met (Power, 1979). In the present study, canonical variate analysis was used to detect broad trends of geographic variation as implied by available samples and the nature of localities.

All samples studied are from regions located between latitudes 15°N and 10°S. As this equatorial belt is enclosed in the tropical zone of Africa, its history is known from the Miocene (25 ------ 12 million years ago), when most of Africa was covered by forest extending through Egypt and Arabia into India and southeast Asia (Beaufort, 1951). Accordingly, a homogenous fauna occurred in the

whole area. Much of the rain forest disappeared, however, when the moist interlude of the Miocene and early Pliocene gave way to a dry period. Some rain forests remained in West, Central and East Africa, but elsewhere forest was replaced by savanna.

Booth (1954) recognized three forest blocks; the high forests of western Ivory Coast, southeastern Guinea and southern Sierra Leone, generally known as the Guinea forest block and shown in Fig. 5 as the Western region. This forest block is distinct and separated from the high forest in Gabon, Equatorial Guinea and the Cameroun south of the Sanaga River by the Dahomey Gap. Booth (1954) has shown that the width of the Dahomey Gap must have fluctuated considerably during the Quaternary but it served to keep high forests of Western regions isolated from high forests of the West Central and East Central regions. The third forest block recognized by Booth is in the northeastern or Upper Congo. These forest refugia are considered by Beaufort (1951), Moreau (1952) and Booth (1954) to be isolated habitats or refugia suitable for endemic speciation.

For the purpose of this study it is helpful to examine geographic variation in the selected taxa of bats in relation to the geographic pattern of forests described above.

The T.(X.) nanula complex

T. calabarensis was described by Hayman (1940) as distinct from T. nanula from a collection made by the Percy Sladen Expedition to the Mamfe Division of the British Cameroons in 1932-1933 and included in a monograph published by Sanderson (1940). The locality, Calabar, is at the edge of mangrove swamps in the south-western part of the Nigeria rain forest. At the time of the expedition, this region was part of what was known as the British Cameroons. Sanderson (1940: 628) argued that: "It becomes abundantly clear that the Western forests of Africa are clearly divided by a number of faunistic breaks or natural barriers of varying efficacy. It must be borne in mind that the rain forests can, and should, be regarded as almost complete faunistic islands."

The concept of faunistic islands or isolated forest refugia, if valid in rodents and other small terrestrial mammals, does not necessarily apply to highly mobile volant bats. Furthermore, forest refugia as such may not be completely isolated. For example, Robbins (1978), who examined satellite photographs taken in 1973, confirmed the presence of isolated patches of high forests within the Dahomey Gap area. In addition, Robbins also demonstrated that the Dahomey Gap has had little influence as a faunal barrier on the distribution of high forest mammals in West Aftica. It was in fact the Volta and

Niger rivers that influenced mammalian distribution. Beaufort (1951) stated that the Niger, the Congo and the Nile rivers were barriers to the dispersal of terrestrial mammals, so that distinct but related species and subspecies are found on either side of these water courses. However, neither rivers nor large bodies of water have proved to be effective barriers to the dispersal of bats. Beaufort (1951: 113), discussing the fauna of Madgascar, stated, "the distribution of bats is of less zoogeographical importance than that of the land mammals, for the sea does not form an absolute obstacle to their dispersal."

In the discriminant analysis of geographic variation of the T. nanula complex the Cameroun sample is morphologically related to the Benin sample even though separated geographically by the Dahomey Gap. Perhaps gene flow between Cameroun and Benin populations was not interrupted by the Dahomey Gap, in that populations of bats in these patches of forest in the Gap may link the above two localities. Moreover, grasslands and forest patches bordering rain forests may be viewed as transitional zones (Cloudsley-Thompson, 1969). Many animals from time to time enter such transitional zones from the savanna, so that clearings and forest edges tend to be more densely populated.

Because the Cameroun sample is from the edge of the high forest, its link with the Benin sample is expected. Nevertheless, phenetic analysis also showed that the Benin sample is related to the Niangara sample in the East Central region. Bats of the two samples are wooded-savanna dwellers, and since the Dahomey Gap is of recent origin (10,000 years ago; Moreau, 1969), bats from the East Central region may have invaded the Gap and come in contact with foraging individuals of western populations so that the taxa had an essentially continuous range.

Furthermore, morphological similarities between the East African forms (Kenya and Uganda) as implied by the minimum spanning tree and the subsets procedure is explainable by the geographical proximity of these populations.

In this study, the association between character variations and environmental data could not be tested because such data are not yet available. Moreover, analyses of character variation do not show consistent clinal trends among the above samples.

Morphological similarities among all samples and absence of obvious geographic barriers among localities suggest that variations among populations may be due to natural variabilities within populations of the same species. Moreover, no clear distinguishing characters are detected

between T. nanula and T. calabarensis, and therfore, I agree with Rosevear (1965) that the two taxa are conspecific.

The T.(X.) leonis complex

In this complex the West African sample is composed mainly of specimens collected from Sierra Leone and Ghana. This sample represents T. leonis. East African sample is represented by T. brachyptera from the Budongo Forest, Uganda. It is not inconceivable, therefore, to think of T. leonis and T. brachyptera as West and East African races, respectively, because of their resemblance to each other. This is not without precedence. Peterson (1971) reviewed the systematic status of T. bemmelini of West Africa and T. cistura of East Africa. In view of their demonstrated similarities, Peterson regarded T. b. bemmelini as the western representative of the species and T. b. cistura as the eastern race.

However, the systematic status of T. leonis is not so easily resolved. Definition of western and eastern races is made difficult by the description of a taxon from East Central Africa. This is the species described by Allen (1917) from Medje, Zaire as Nyctinomus ochraceus. In his original description, Allen (1917) distinguished T. ochraceus and T. leonis from the same locality because of pelage colour differences: T. leonis was much paler

than T. ochraceus, which had a bright Ochraceus-Orange colour covering the venter. However, the type specimen (AMNH 48821), a female, was compared by Allen with T. thersites, a related but distinct species. Later, Koopman (1965) pointed out the close resemblance of T. ochraceus to T. leonis and considered T. ochraceus to be a race of T. leonis. Koopman consequently referred the two specimens recorded by Allen to the subspecies T.l. ochraceus (Fig. 39).

Furthermore, Rosevear (1965: 343) mentioned specimens in the British Museum (Natural History) that showed marked colour variations:

"(BMNH 9.10.2.4) collected by Bates at Bitye, Cameroon, is rich deep red-brown on the back, the chest and belly creamy-white slightly more orange towards the flanks with an orange-brown strip on the wing. This is in some degree matched by four specimens, also from the Cameroon, (Eshobi) .....with a greater amount of orange in the chest and flanks below."

Rosevear stated that these specimens could either be different species or colour varients of T. leonis although measurements and the skull supported the latter view, which Rosevear subsequently adopted. I examined specimens from Cameroun, the Central African Republic and Ghana and found all to show striking colour variations (Fig. 40). Also, specimens examined from the Budongo Forest, Uganda, show colour variations not related to sex (Fig. 41).

Fig. 39

Dorsal (A) and ventral(*A) views of T. leonis from Panga, compared to T. ochraceus from Medje, Zaire. (B) dorsal (*B) ventral view.

Fig. 39

A B

* *

A B

Fig. 40

Colour variations in the ventral pelage of T. leonis from (A) Cameroun (B) Central African Republic and (C) Ghana.

Fig. 40

Fig. 41

Dorsal and ventral colour variation in T. leonis (=brachyptera) from the Budongo Forest, Uganda.

Fig. 41

In addition, Koopman (1965: 21) mentioned a note left with a skin from Panga, Zaire, written "perhaps by John Eric Hill in which it was stated (Probably same as Mops ochraceus but taken in the fall)". Therefore, Koopman thought that the colour difference might be seasonal. On the other hand, if variation in colour is seasonal, I could not discover consistent seasonal differences even though I examined specimens collected at different times of the year.

The pattern of colour variation in this complex may be summarized in the following four categories:

1. Eastern Region: represented by specimens from Budongo Forest, Uganda, with white and Ochraceous-Orange venters.
2. East Central Region: represented by specimens from Medje, Zaire with Ochraceous-Orange venters.
3. West Central Region: represented by specimens from Cameroun and the Central African Republic with Ochraceous-Orange venters.
4. Western Region: represented by specimens from Ghana and Sierra Leone with White and Pale Buff venters (Fig. 42).

Colour variation, however, does not necessarily indicate significant morphological differences among these four groups, as such colour differences could also represent polymorphism or moulting (Starrett, 1976).

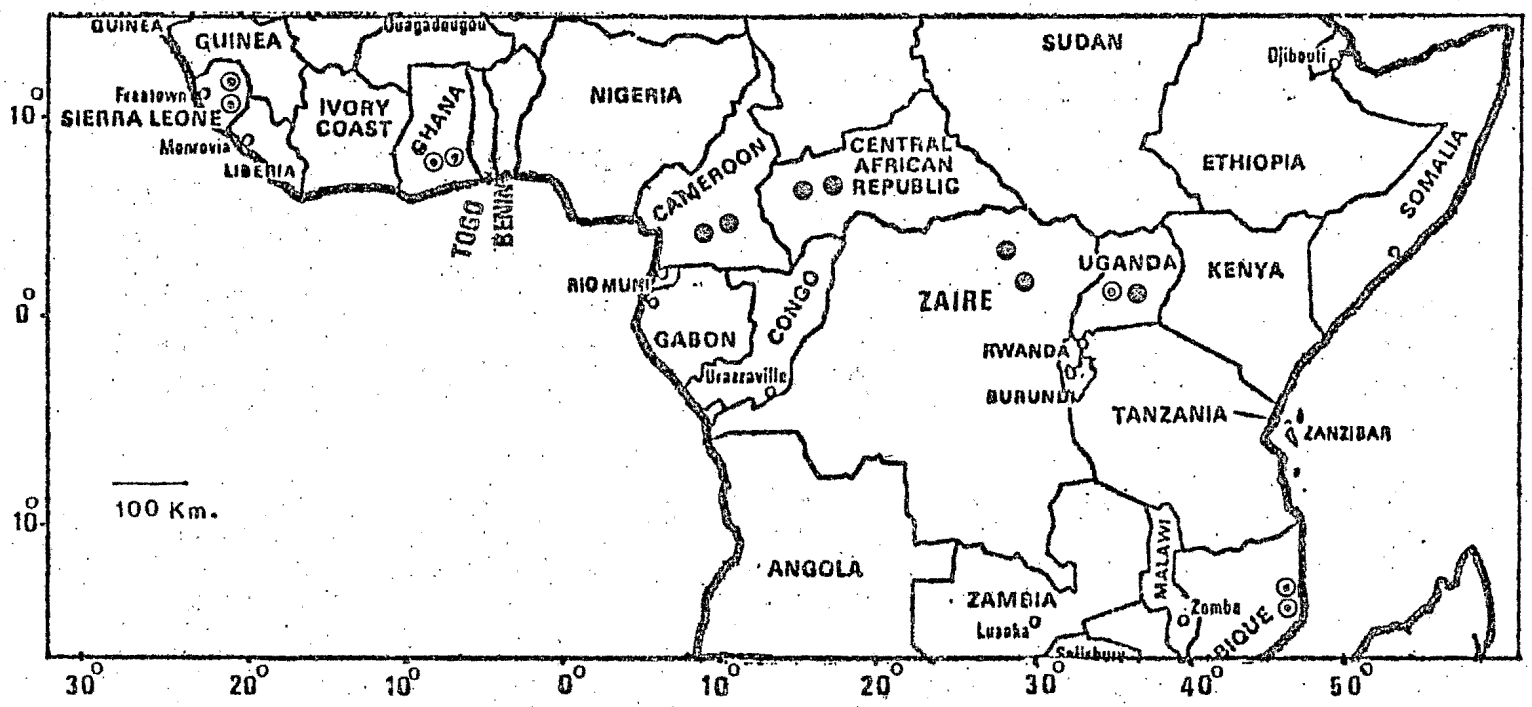
Fig. 42

The distribution of T. leonis complex according to ventral pelage colour.

● Ochraceous-Orange

⊙ White

Fig. 42


GUINEA
Ouagadougou
GUINEA
Freetown
SIERRA LEONE
Monrovia
LIBERIA
IVORY COAST
GHANA
TOGO
BENIN
NIGERIA
CAMEROON
CENTRAL AFRICAN REPUBLIC
SUDAN
Djibouti
ETHIOPIA
SOMALIA
RIO MUNI
GABON
CONGO
Brazzaville
ZAIRE
UGANDA
KENYA
RWANDA
BURUNDI
TANZANIA
ZANZIBAR
100 Km.
ANGOLA
ZAMBIA
Lusaka
MALAWI
Zomba
Salisbury
MOZAMBIQUE
10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°

Harrison (1959: 224) reported colour variations in T. niveiventer from southern Zaire: "An adult male from Egzambo exhibited a remarkable erythrism by being throughout bright orange-brown, uniformly lighter and more orange ventrally". Another example from the same locality was dark "chocolate brown dorsally with the distal central belly white". Verschuren (1957) doubted the validity of the various subspecies based on colour variation in these bats. G. M. Allen (1939: 368) mentioned that the colour of Myotis lucifugus follows Gloger's rule. In humid parts of North America and Mexico M. lucifugus occurs with a "brassy brown" colour, whereas in the drier parts of the Southwest of America it becomes "pale, whitish or buffy". Even the striped pattern of Burchell's Zebra, Equus burchelli in South and East Africa has been shown by Mettler and Cregg (1969) to vary in a continuous gradation. The black stripes that cover the entire body in northern populations gradually disappear from the body in southern populations.

Colour variation in this complex could not be related to Gloger's rule because White and Ochraceous morphs occur in the same population from the same locality, especially in the sample from the Budongo Forest, Uganda. In T. nanula, however, colour variation follows Gloger's rule. Specimens collected from the open savanna land of Kenya, the Sudan and Benin have pale colours in contrast to specimens collected from Cameroun that are brightly

coloured. Specimens of T. nanula collected from the Budongo Forest show a pattern of variable colouration similar to that in T. brachyptera from the same locality (Fig. 43).

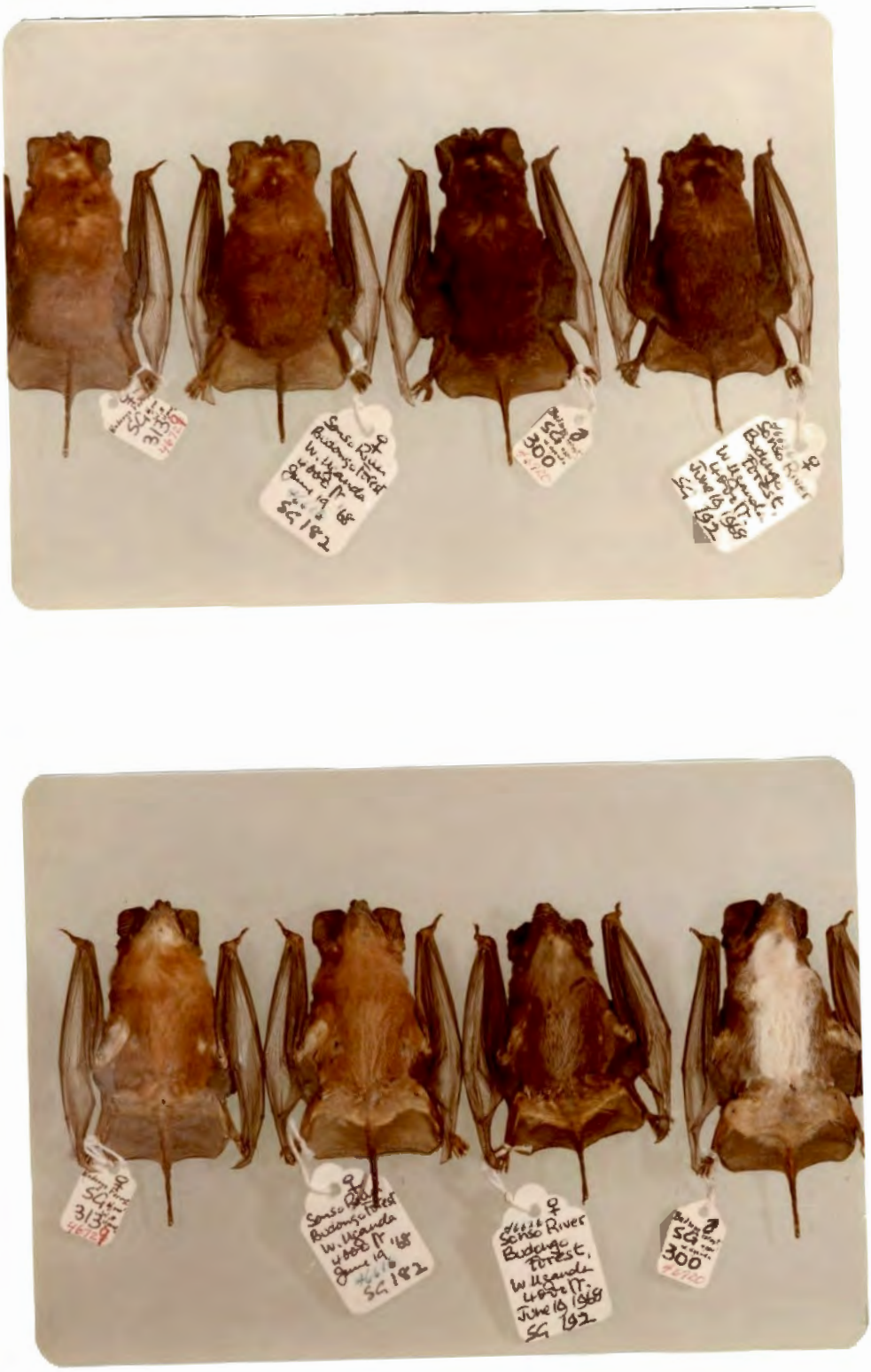
In addition to colour variations in the T. leonis complex, characters in males and females gradually increase in size in a west-east cline, with West African samples averaging smaller in some characters (Tables 13 and 14). It is thus tempting to think of the West African sample as a distinct group. Endler (1977) argued that isolation may result from distance rather than by geographical, ecological or temporal factors. Huxley (1942) and Rensch (1960) also stated that in many cases the extremes do not successfully interbreed. If some catastrophe or change in climate resulted in the extinction of intermediate populations, survivors would be good biological species. On the other hand, if the species described as T. ochraceus if valid, then populations could be represented as follows:

1. T. brachyptera brachyptera: to represent the trinominal taxon, as the name brachyptera antedates both ochraceus and leonis. It also represents the Eastern African race from Mozambique to Uganda.
2. T. b. ochraceus: representing populations from Central Africa, with a range from Zaire and Central African Republic to Cameroun.
3. T. b. leonis: representing populations from West Africa from Nigeria to Sierra Leone (Fig. 42).

Fig. 43

Dorsal and ventral colour variation in T. nanula from the Budongo Forest, Uganda.

Fig. 43



This subdivision of the species cannot be easily substantiated. Examination of the results of the generalized discriminant analysis for males and females reveals a complicated picture. The minimum spanning tree of males linked samples from West Africa with Cameroun, Medje with Uganda, and Uganda with Cameroun. But the subsets procedure grouped Uganda and Cameroun in a nonsignificant subset (Fig. 20). The suggested morphological similarities between these two samples and hence their phenetic association is unusual, e.g., the Cameroun sample joining Uganda instead of Medje. But this relationship may be correlated with the extension of lowland habitats. Excluding West Africa, the lowland fauna and flora is confined to the coastal rim of the continent, the Congo basin and the southern portion of the Sudan. Moreover, the fauna and flora of the Cameroun mountains closely resembles that of the highlands of East Africa, although the two are separated by some 1925 km. of unbroken lowland forest (Moreau, 1952). Furthermore, forest dominanted by Isoberlinia sp. extends in a belt from Senegal to Uganda, curves south of Lake Victoria through western Tanzania and reaches the Miombo savanna that extends from Angola to Mozambique. Moreover, the Coastal scrub and grassland zone of the Guinea savanna that extends between the Atlantic Ocean and the inland tropical forest is similar to the Miombo savanna except that the Miombo is floristically richer than the Guinea savanna.

Hence, because the broad extent of these forests and continuity of habitats without any apparent geographic barriers, it is difficult to establish arbitrary boundaries between populations of any species which might consist of distinct and reproductively isolated populations as proposed above. In addition there is no evidence to suggest that gene flow has been interrupted spatially or temporaly between the West and the West Central African population represented by the Cameroun. Dobson (1876) and Rosevear (1953) reported T. leonis from Nigeria and Fernando Po. As I find no tangible geographic variation meriting recognition by description of new subspecies of various populations of T. leonis, I view T. leonis as a single widespread panmictic species.

The T.(X.) thersites complex

In this complex two taxa have been recognized. Thomas (1903) described an adult male collected by G. L. Bates from Efulen, Cameroun, as a new species Nyctinomus thersites. Thomas (1903: 635) mentioned that "by Dobson's synopsis this bat comes near N. pumilus but may be readily distinguished from that species by its large size and the many peculiarities external and cranial". However, Allen (1917) described a new taxon from Avakubi, Zaire as Mops (Allomops) occipitalis. Allen pointed out the similarities between N. thersites and M. occipitalis but only cited the degree of separation of

the premaxillae as a difference. In the original description of N. thersites, Thomas (1903: 635) stated that "the premaxillae are separated, but opening between them small". In Allen's (1917: 476) description of M. occipitalis "the premaxillae are fully ossified in four of them (specimens) and in the other two (one of them the type and the most mature specimen) there is a slight opening behind and between the incisors". Among specimens that I examined including the holotype (AMNH 48851), the opening between the upper incisors may be covered over by the soft palate, giving a false impression that the emargination is absent. I therefore consider this distinction to be artificial. Moreover, Koopman (1965) reviewed the status of T. occipitalis and tentatively considered it to be a subspecies of T. thersites because of the great distance separating type localities of the two taxa.

Analysis of geographic variation did not reveal any clear differentiation among samples from West, Central and East Africa. The male sample from Cameroun was linked by the minimum spanning tree to samples from Uganda and Medje, Zaire, indicating similarity of the Cameroun sample to both Uganda and Medje. This resemblance is understandable in view of the continuous lowland forest that extends from the West Central region to East Central Africa and apparent lack of opportunity for differentiation of populations.

But, no link was made between the Medje and Uganda sample, although these two localities are proximal. This distortion may be caused by the few samples from Medje. In addition, I cannot readily explain apparent similarities suggested by the minimum spanning tree between Ivory Coast and Cameroun samples as Ghana is closer to the Ivory Coast but resembles those of the Ivory Coast no more than those from Cameroun. Moreover, no link was detected between Ghana and Cameroun in male and female samples although geographically Ghana lies between Cameroun and Ivory Coast. Furthermore, the Ghana and Uganda samples, although not separated along the second canonical axis, are widely separated along the first axis by differences in condyloincisive length and fourth metacarpal in males and lower canine height and mandibular toothrow in females (Figs. 24, 26).

Clinal variation was not detected, although the Cameroun sample averaged smaller in size relative to East-West samples. However, these differences do not necessarily indicate that the populations compared have differentiated at the species level because in male and female samples, Uganda is connected with Cameroun in a geographically explainable pattern. Also in females, the West African localities are related in a concordant pattern except for the slight distortion implied by the minimum spanning tree that linked the Ivory Coast and the Cameroun samples. As there was no evidence of geographical or ecological isola-

tion in these samples, observed variation is attributed to that of natural populations of the same species. Hence, T. occipitalis is regarded as a synonym of T. thersites, as was previously suggested by Rosevear (1965).

T.(X.) spurrelli

Males collected from three localities did not significantly differ, but females differed significantly. Phenetic similarity between samples from Ivory Coast and Ghana is shown by the overlap of the two populations in the histogram given in Fig. 28, whereas the Cameroun sample is separated from the other two localities.

The low number of significant character variations detected by the SS-STP procedure (five of 31 characters) suggests that the species has not undergone appreciable differentiation detectable by univariate procedure. In addition, the minimum spanning tree connecting group centroids and superimposed on the map of geographic locations produced a pattern coinciding with the geographic location sequence (Fig. 29). However, data presented here extend the range of the species as far east as the Central African Republic and as far west as the Ivory Coast.

Geographic variation examined in the selected taxa did not reveal evidence suggesting that any populations studied have become isolated by virtue of geographic interruption of gene flow. Moreover, subspecies as tentatively

recognized by Koopman (1965) are not tenable because examination of samples in intermediate zones between type localities revealed the existence of a continuous range of distribution in all taxa involved. Colour and size variation did not show any obvious morphological trends. Although the kind of variations revealed here by univariate and multivariate procedures is standard in studies of phenetics of discordant populations (Barlow and Power, 1970), it is preferable to describe these variations in terms of variability exhibited by natural populations instead of referring to them by subspecific names. As there are no generally established and accepted ways to delimit subspecies (Sokal, 1965), one questions the usefulness of recognizing T. calabarensis, T. ochraceus and T. occipitalis as subspecies of T. nanula, T. leonis and T. thersites, respectively.

Phenetic Similarities in the Xipho-Mops Complex

Similarities based on shape and size were emphasized by the use of correlation coefficients and average taxonomic distance, respectively. Correlation coefficients, summarized in phenograms, produced different hierarchical groupings for males and females. As similarities are assessed according to shape, phenograms may be affected by sampling factors. In T. demonstrator there were only five males and two females, and T. trevori was represented by only one male and three females.

The small species, T. nanula and T. spurrelli, grouped together, whereas the larger species, T. thersites, T. condylura and T. demonstrator were grouped in a separate cluster. T. thersites and T. condylura are strikingly similar in the shape of the basisphenoid pits and in the width of the septum that separates them. T. demonstrator and T. condylura have similar wing measurements and skulls of similar shapes. In a third cluster T. leonis and T. "subleonis" grouped as a consequence of similarities in the shape of the basisphenoid pits and the degree of reduction of the last upper molar. The last cluster is composed of T. trevori, T. congica and T. midas, the largest in the group. T. congica and T. trevori show similarities in wing structure and shape of the skull. They have a closed palate with small perforations and show similarities in the shape of the brain case.

When species were ordered by size in phenograms of average taxonomic distance, hierarchical groupings of males and females were identical.

The first cluster grouped T. nanula, T. spurrelli and T. "subleonis". In this cluster, T. spurrelli is the smallest, and T. "subleonis" is the largest, whereas T. nanula occupies an intermediate position. The second cluster is comprised of T. leonis, T. thersites, T. demonstrator and T. condylura, and the third cluster grouped T. trevori, T. congica and T. midas.

The same pattern of relationship was apparent in the PCA/MDSCALE configuration. The subsets procedure grouped T. nanula and T. spurrelli in one subset and enclosed them in a larger subset encompassing T. "subleonis". T. thersites and T. leonis were also included in one subset. The two species are similar, and, in the absence of distinct size differences, Rosevear (1965) suggested that T. leonis and T. thersites are conspecific and represent colour variants. Rosevear also cited T. S. Jones (pers. Comm.), who noted that at Newton, Sierra Leone, T. thersites and T. leonis roosted together under a roof and emerged togehter at dusk from the same hole. After examining large samples of both T. leonis and T. thersites, I am convinced that the two are distinct species. Perhaps the most important features separating T. leonis from T. thersites are the nude posterior dorsolateral surfaces in T. thersites (Fig. 44) and

Fig. 44

Dorsal(A) and ventral(A*) views of T. occipitalis from Medje, Zaire, compared to T. thersites from the Cameroon. (B) dorsal (B*) ventral views.

Fig. 44


57160
CAMEROUN
67 KM. WEST of AYOS
TL TV HA E WT
100 31 10 19 22.5
FA 382 NETTED ON FOREST ST
WS 290 WHILE EMERGING FROM FO

A B


DEPARTMENT OF MAMMALOGY — ROYAL ONTARIO MUSEUM
PURCHASED
0958
57160

* *
A B

the well developed and continuous lambdoidal crest in T. thersites which is interrupted in T. leonis. Moreover, Peterson (pers. comm.) who examined the male holotype of T. leonis (BMNH 62.12.23.3) stated that T. leonis has distinctive basisphenoid pits. The pterygoid fossa forms a trough that extends anteriorly without interruption and the dividing septum between the pits forms an elongated triangle progressing at the apex to join the dividing septum of the posterior palate.

It is possible that T. thersites or T. leonis could be a later name for T. brachyptera (Peters, 1852). The taxonomic status of T. brachyptera has remained questionable. The holotype, which was deposited in the Berlin Museum, has been lost, and except for the descriptions given by Peters (1852) and Dobson (1876, 1878), the holotype has not been referred to subsequently. Moreover, additional collections have not been made from the type locality (Mozambique). In their study of the mammals of Mozambique, Smithers and Labao Tello (1976) suggested that T. brachyptera might be referred to T. thersites. Specimens from Sierra Leone regarded by Dobson (1876, 1878) as Dysopes brachyptera were later included by Thomas (1908) in Nyctinomus leonis. The comparison given in Table 23 shows that T. brachyptera is more similar to T. leonis than to T. thersites, even though differences in skull length are pronounced. However, the skull length of a male T. leonis (ROM 46721) is 20.25 mm as compared to that T. brachyptera, which is 21.5. The only other species with a skull length approximating 21.5 mm

are T. demonstrator and T. condylura, but with forearms of 45 mm they are obviously larger. In the original description of T. brachyptera by Peters (1852: 51) there are two obvious characters that do not apply to T. thersites, "on the middle of the belly from the neck to anus, the colour is grey..... the hairs on the throat are all white .... and dorasIly the hairs spread to the side of the flying membranes". In T. thersites, ventrally, hairs are light Mummy Brown and dorsally the pelage does not spread to flying membranes as the posterior dorsolateral surfaces are completely nude and without hair. The description, therefore, seems to apply to T. leonis. Apart from similar measurements, colour of the ventral pelage of T. leonis varies from white to gray or even sometimes to Ochraceus-Orange, besides, the hair extends onto the wing membrane, and there are no bare areas on the dorsum as in T. thersites (Fig. 44). It is clear that Dobson's (1876, 1978) specimens of T. brachyptera from Sierra Leone which were later referred to T. leonis by Thomas (1908), are most certainly T. brachyptera. Dobson (1876: 702) had most probably seen the holotype, since he stated that "the following monograph of the species is the result of my examination of a large number of specimens (including most of the types) preserved in the British Museum, in the Museums at Leyden, Berlin and Paris....".

Furthermore, T. thersites has not been recorded from anywhere east of the Budongo Forest, Uganda, whereas T. brachyptera has been recorded from northern Kenya by Dobson (1880) and from Bagamoyo, Zanzibar Island by Swynnerton and Hayman (1951). Because of the excellent description of T. brachyptera given by Peters (1852) and the meticulously drawn figures and their agreement with T. leonis, I consider T. brachyptera to be an earlier name for T. leonis. I therefore consider T. leonis to be a synonym of T. brachyptera (Article 24, International Commission of Zoological Nomenclature, 1964).

The relationship between the three large taxa (T. trevori, T. congica and T. midas) was illustrated by the minimum spanning tree. T. trevori and T. congica were included in one subset. Peterson (1972) studied in detail the relationship between these taxa. Although T. congica is larger than T. trevori in wing and skull measurements, Peterson showed that they were similar in the shape of the basisphenoid pits and the location and conformation of the six palatal ridges. He also showed that T. congica is intermediate in size between T. trevori and T. midas, although the skull of T. midas is larger.

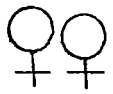
The minimum spanning tree also linked T. demonstrator and T. condylura with taxa placed by Koopman (1975) in the subgenus Xiphonycteris. These two taxa also link with the large species T. trevori, T. congica and T. midas in the subgenus Mops.

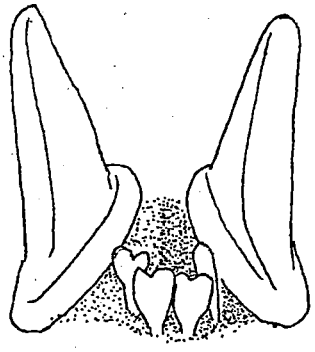
It seems, therefore, that the closeness of phenetic similarities of these taxa now in the two subgenera Xiphonycteris and Mops warrant their inclusion in a single subgenus rather than two. The subgenus Xiphonycertis was first established as a genus with the contention that the species in it possessed a dental formula different from that possessed by the species in the subgenus Mops. De Vree (1969: 279) stated that "the original differences between Xiphonycteris and Tadarida became severely invalidated in the first place by the lack of any enlargement of the canines in the females of Xiphonycteris and secondly by the fact that the presence of only a single pair of lower incisors seems to be variable". I examined the number of lower incisors in a large number of T.(X.) spurrelli and found it to vary. For example, in four females (USNM 424909, 424917, 424919 and ROM 56140) there are two pairs of lower incisors; in another female (ROM 57171) there are three incisors, a number found in a specimen examined by Kock (1969a;SMF 22123; Fig. 45). The same pattern of variability was also detected in males; in two specimens (ROM 57035 and 57051) three lower incisors were present (Fig. 46). It appears, therefore, that the main diagnostic character upon which the genus was established is not valid.

Normally the use of numerical techniques employed here does not rule out orbitrary judgements regarding higher categories.

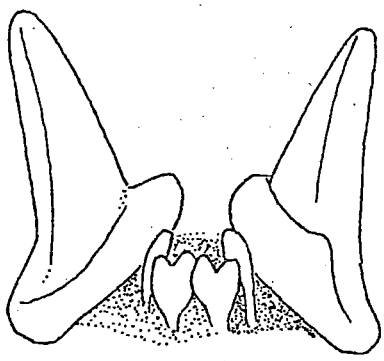
Fig. 45

Variations in the lower incisors of female Tadarida (Xiphonycteris) spurrelli.

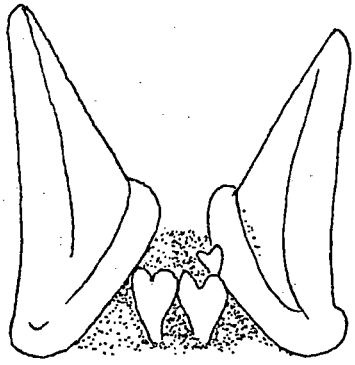




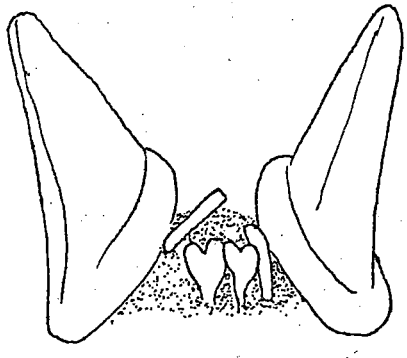
USNM 424909



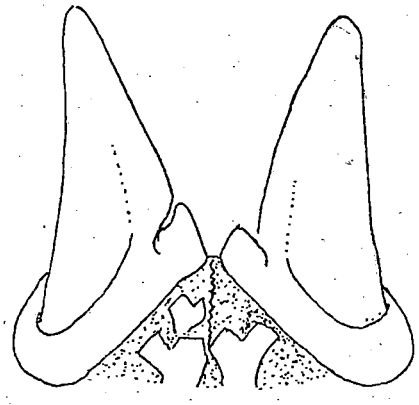
USNM 424917



ROM 57171

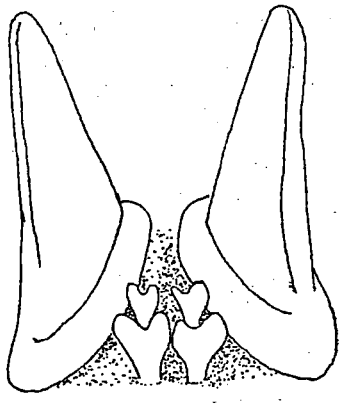


USNM 424919



SMF 22023

1 mm.

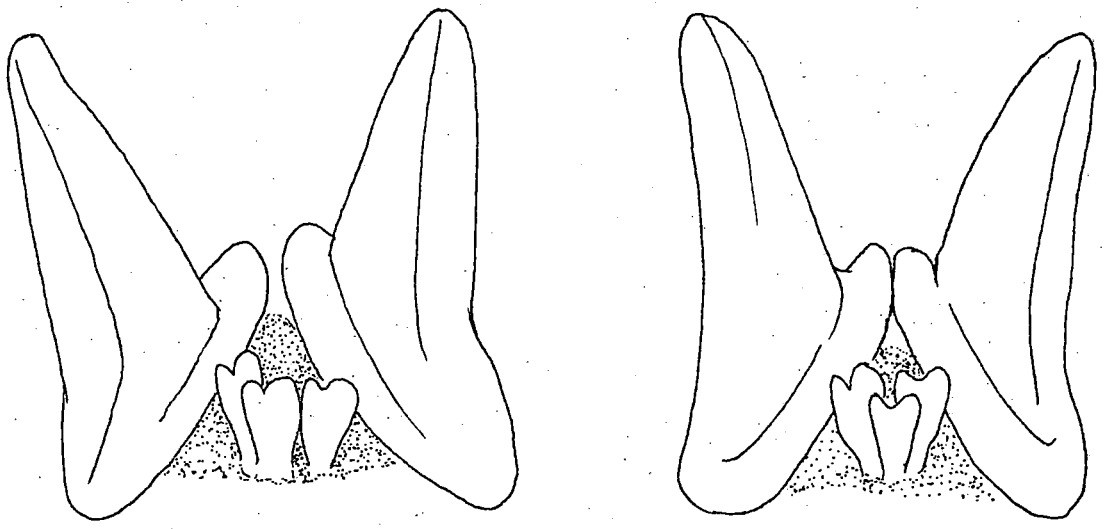


ROM 58140

Fig. 46

Variations in the lower incisors of male T. (X.) spurrelli.

♂♂



ROM 57037

ROM 57051

1 mm.

Thus a review of criteria by which the reallocation of the genus Xiphonycteris to a subgeneric rank is warranted. In his argument for the establishment of the subgenus Xiphonycteris, Koopman (1975: 420) stated, "thus conceived T. (Xiphonycteris) would include forms with a reduced last upper molar (and therefore previously placed in the subgenus Mops) and with a well-developed anterior palatal emargination (as in the subgenus Tadarida). The subgenus Mops would then be restricted to the species with a reduced last molar and a closed palate".

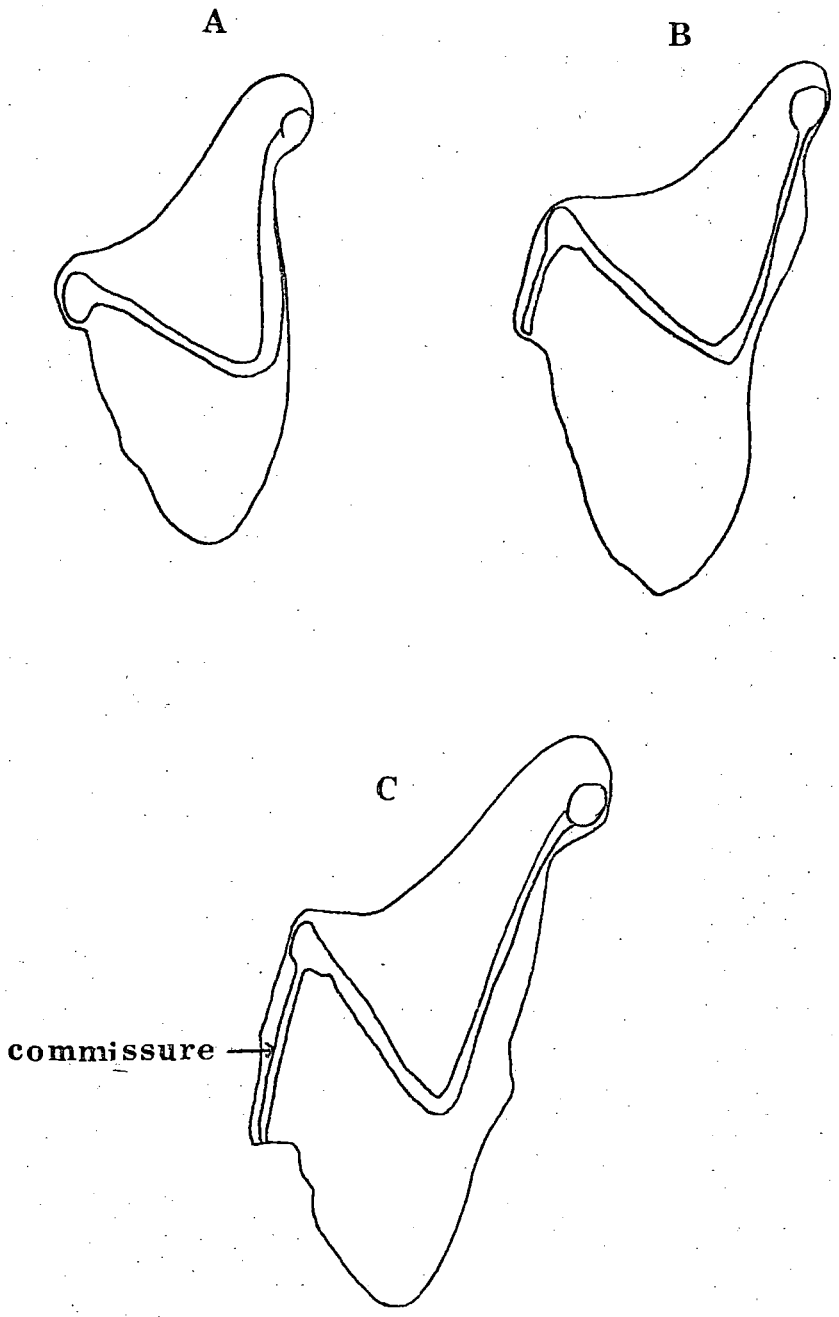
The presence or absence of a palatal emargination, combined with the reduction of the third commissure on last upper molar, is a questionable diagnostic character. According to these criteria, taxa could be grouped into small subdivisions that do not qualify as subgenera. For example:

1. Taxa with no third commissure on the last upper molar and an open palate: T. nanula and T. spurrelli.
2. Taxa with no third commissure on the last upper molar and a closed palate: T. midas and T. demonstrator.
3. Taxa with a partially reduced third commissure on the last upper molar and an open palate: T. thersites, T. brachyptera and T. "subleonis".
4. Taxa with a partially reduced last upper molar and a closed palate: T. congica, T. condylura and T. trevori (Fig. 47).

Fig. 47

Variations in the length of the commissure of the third upper molar (M^3)(of the right side) in (A) T. spurrelli, T. nanula, T. demonstrator and T. midas. (B) T.leonis, T. thersites, T."subleonis", T. condylura, T. trevori and T. congica.(C) length of commissure in taxa in the subgenus Chaerophon.

Fig. 47

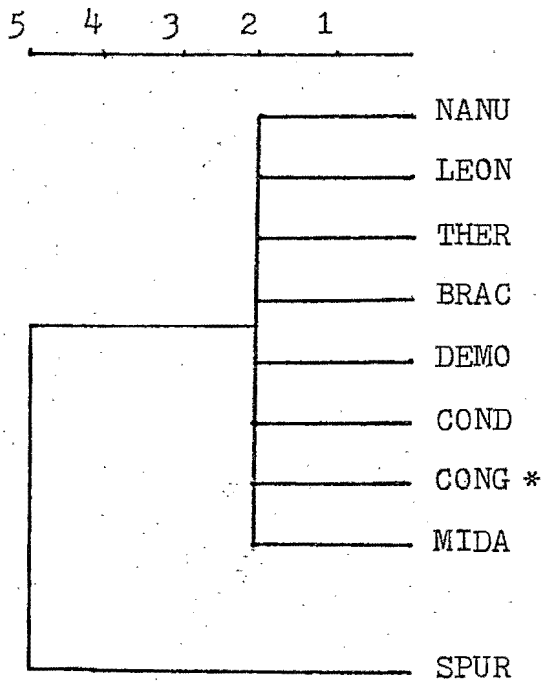


Furthermore, Freeman (1977), although not agreeing with Koopman as to the establishment of the subgenus Xiphonycteris, advocated the upgrading of all the subgenera in the genus Tadarida to a generic level. My main concern here is not to confirm or to refute this view, but to detect sufficient differences that separate groups of species into distinct divisions. In my judgement, a subdivision of the subgenus Mops would only add more confusion. As I consider the subgenus Xiphonycteris, to be invalid, I am inclined to remove all taxa that were previously placed in it to be included in the subgenus Mops and to be separated from other taxa in other subgenera in the genus Tadarida by the reduction of the third commissure of the last upper molar and not by the palatal emargination. In the subgenus Chaerophon the palate is closed, but the last upper molar is not reduced as in the subgenus Mops. It is also not reduced in the subgenera Tadarida and Mormopterus. Therefore, the reduction of the commissure on M^3 serves to separate taxa in the subgenus Mops from taxa in other subgenera in the genus Tadarida. A summary of the proposed classification of the taxa studied here as compared to classifications proposed by Rosevear (1965), Hayman and Hill (1971) and Koopman (1975) is given in Fig. 48.

Fig. 48

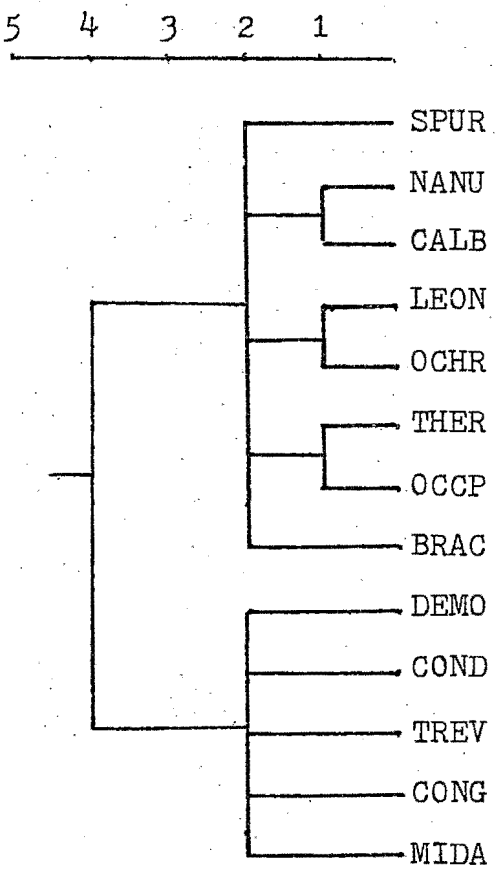
Dendrograms depicting classifications proposed by Rosevear (1965)Hayman and Hill (1971), Koopman (1975) compared to classification suggested by this study. Junctions between stems indicate taxonomic levels. The following arbitrary similarity coefficients were assinged to formal taxonomic levels : (1) subspecies (2)species (3)subgenus (4)genus and (5) family. See text for OTU abbreviations.

Fig. 48

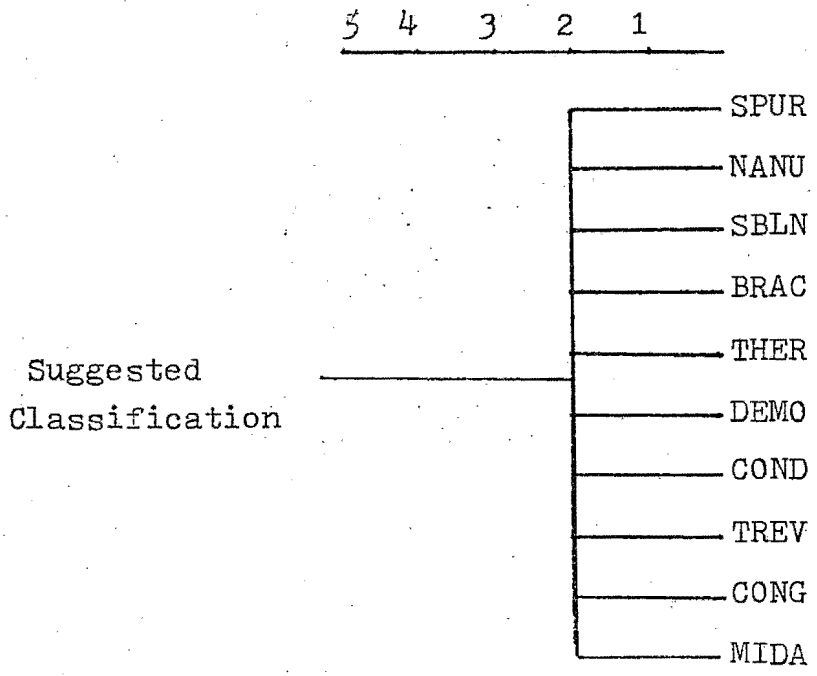


Rosevear(1965) and
Hayman and Hill(1971)

* including TREV.



Koopman(1975)



SUMMARY

1. Sexual dimorphism was detected in T. spurrelli, T. nanula, T. leonis, T. thersites, T. "subleonis", T. condylura, T. congica and T. midas. Males are generally larger than females, and species of smaller size are more dimorphic than are larger species.

2. Study of phenetic similarities among taxa in the subgenus Xiphonycteris revealed the existence of three distinct groups: T. nanula (including T. calabarensis), T. spurrelli and T. subleonis ; T. leonis (including T. ochraceus and T. brachyptera); T. thersites (including T. occipitalis).

3. Specimens tentatively recognized as T. "subleonis" were compared with T. nanula and T. leonis and were found to be a distinct species.

4. Studies of geographic variation in selected taxa in the subgenus Xiphonycteris did not yield evidence of speciation or subspeciation in the taxa studied, and only five species were found to be valid: T.(X.) nanula, T.(X.) leonis, T.(X.) thersites, T.(X.) spurrelli and T. "subleonis".

5. Investigation of phenetics of taxa in the subgenus Mops revealed their morphological similarities. The number of lower incisors in T. spurrelli was found to

be so variable that the genus Xiphonycteris is considered to be invalid. The criterion by which the genus Xiphonycteris was re-allocated to a subgeneric rank was also examined and proved to be invalid.

6. Taxa previously removed from the subgenus Mops and included in the subgensu Xiphonycteris were grouped under the subgenus Mops.

7. The East Africa taxon T. brachyptera is considered an earlier name for T. leonis and it is recommended that T. leonis be treated as a synonym of T. brachyptera.

8. The subgenus Mops is therefore considered to include the following species: T. spurrelli, T. nanula, T. brachyptera, T. thersites, T. "subleonis", T. demonstrator, T. condylura, T. trevori, T. congica and T. midas.

SPECIES SYNOPSES

Tadarida (Mops) petersoni, sp. nov.

Holotype

Male, adult in alcohol with skull extracted, ROM 55813, from 15 km. S. Kumba, Cameroun, (04° 39'N. 09° 26'E.), collected January 27, 1970, by Dr. R. L. Peterson (field no. 0364).

Specimens Examined (36)

Cameroun: Topotypes 6 ♂♂, 12 ♀♀ (ROM); 30 km. N. Buea Station, Mawutu village 6 ♀♀ (ROM); 6 km. S.E. Eseka 1 ♂, 1 ♀ (AMNH): 1 ♀ (CM); 30 km. E. Nanga Emboko 1 ♂, 1 ♀ (AMNH): E. okola 1 ♂ (AMNH).

Ghana: 12 km. N.E. Kade 4 ♂♂, 2 ♀♀ (ROM)

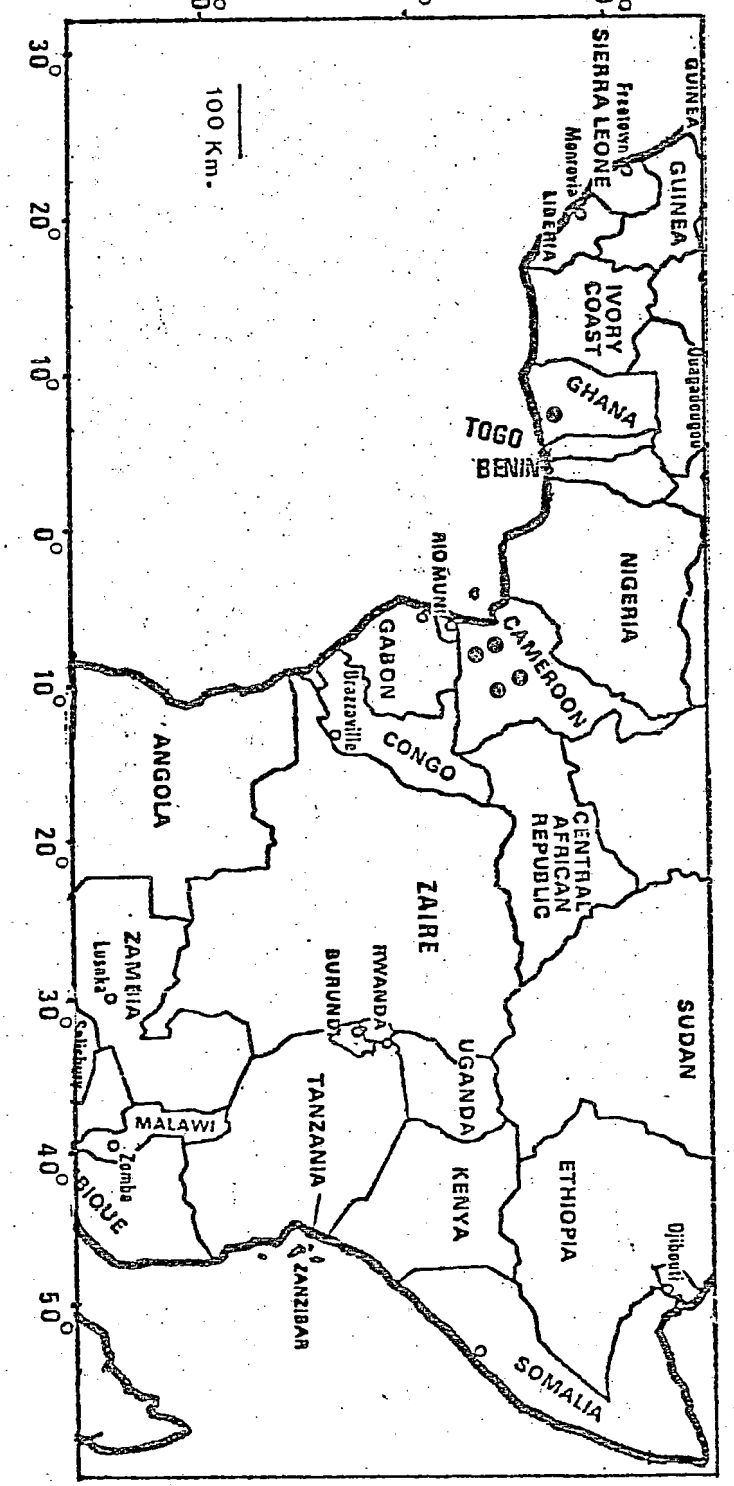
Distribution

Known from Cameroun and Ghana (Fig. 49).

Diagnosis

Dorsal pelage uniform Prout's Brown extending to the sides of the neck immediately ventral to the antitragus. Base of hairs pale brown, darker distally. Ventrally, fur varying from Pale Ochraceous-Buff on chin and throat to light Pinkish Cinnamon on chest and abdomen. Pelage

Fig. 49
● Distribution of T. petersoni.


10°
0°
10°
30°
20°
10°
0°
10°
20°
30°
40°
50°
100 Km.
GUINEA
SIERRA LEONE
Freetown
Monrovia
LIBERIA
GUINEA
IVORY COAST
Ouagadougou
GHANA
TOGO
BENIN
NIGERIA
RIO MUNI
CAMEROON
GABON
Brazzaville
CONGO
ANGOLA
CENTRAL AFRICAN REPUBLIC
ZAIRE
SUDAN
ZAMBIA
Lusaka
Salisbury
BURUNDI
RWANDA
UGANDA
MALAWI
Zomba
TANZANIA
KENYA
ETHIOPIA
MOZAMBIQUE
ZANZIBAR
Djibouti
SOMALIA

Cinnamon-Drab ventrolaterlly along the insertion of the endopatagium to the base of the humerus and femur. Ventral pelage with white basal band, darker distally. Dorsally hair short (about 2 mm), ventrally slightly longer on throat (about 4 mm). Dorsally and ventrally hair extends to the endopatagium. Posterolateral edge of uropatagium sparsely fringed with long bristles (about 6.5 mm).

Feet small (9.0 mm) sparsely covered with hair to tip of toes. Calcar short (6.5 mm). Wing membrane about 3.5 mm above the ankle at the base of the metatarsus. Upper lips thick, with vertical wrinkles. Ears joined on the muzzle by a deep band; tragus small, rectangular (about 1 mm wide and 1.8 mm long), antitragus about 4.3 mm long and 3.3 mm wide; first upper premolar small, in line with toothrow and filling the space between the canine and the second premolar; upper incisors vertical, parallel, separated from canines by pre-canine diastema (about 0.6 mm). Anterior palatal emargination extends posterior to upper incisors (in the holotype covered by the soft palate). Soft palate transversed by five palatal ridges. Third Commissure on the last uppermolar (M^3) reduced, much shorter than second. Lower incisors small bifid and filling the space between the lower canines. First lower premolar as high as second but wider at the base. Basisphenoid pits well defined and oval in shape.

Measurements of the Holotype

Total length, 93 mm; tail length; 27 mm; hind foot, 9 mm; ear, 19 mm; tibia, 13.3 mm (for other measurements see Tables 26 and 27).

Comparisons

Differs from T. nanula in having longer and wider wings and skull; septum separating basisphenoid pits smaller but pits large; smaller canines and narrower postorbital constriction; large brain case.

Differs from T. spurrelli in having longer and wider wings and skull; upper and lower canines without enlarged cingula; higher brain case; longer mandibles.

Differs from T. brachyptera in having smaller wings and skull; shorter upper and lower canines; shorter mandibles; no sagittal or lambdoidal crest.

Remarks

T. petersoni can readily be distinguished from T. nanula and T. spurrelli by the reduction in size of the third commissure on M^3, which is absent in T. nanula and T. spurrelli. However, T. petersoni is similar to T. brachyptera in this character but differs in all measurements (Table 26, Figs. 50, 51 and 52).

Etymology

This species is named in honour of Dr. R. L. Peterson, who discovered it and who has made outstanding contributions to the knowledge of molossid bats, particularly in Africa.

Table 26

A comparison of wing and skull measurements of the holotype (ROM 55813) of T. petersoni with means of 29 T. nanula, 14 T. petersoni and 45 T. brachyptera(all males)

Character	T. nanula $\bar{X}$	Holotype ROM 55813	T.petersoni $\bar{X}$	T. brachyptera $\bar{X}$
FOAR	30.25	33.80	33.79	36.93
3MET	31.08	35.50	35.22	38.69
3M1P	11.61	12.80	13.02	14.89
3M2P	11.29	12.10	12.55	14.70
4MET	30.08	34.40	33.33	37.20
4M1P	9.22	10.60	10.74	11.95
4M2P	7.69	8.10	8.04	8.40
5MET	20.41	22.80	22.59	25.08
5M1P	7.74	8.9	9.15	9.85
5M2P	2.79	2.9	2.85	3.37
GSLN	16.52	17.30	17.08	19.17
CDIN	15.43	15.80	15.94	17.60
PALL	6.74	6.75	6.86	7.68
ZYGO	10.44	10.85	10.97	12.03
MAST	9.90	10.00	10.22	10.98
BBCS	8.34	8.65	8.76	9.54
HBCS	4.77	5.60	5.65	5.86
ROWL	5.96	5.55	5.76	6.72
IOWA	4.52	4.60	4.25	5.32
POCN	3.53	3.35	3.46	3.82
M3M3	7.38	7.25	7.41	8.04
CANM	6.11	5.85	5.99	6.78
CANC	4.74	4.80	4.67	5.35
CANH	3.26	3.10	3.09	3.54
WBSP	0.96	0.71	0.76	0.90
LBSP	0.94	1.20	1.18	1.32
CNIL	11.47	11.35	11.48	12.98
GMLN	11.89	12.30	12.23	13.62
LCAM	6.88	6.60	6.64	7.48
LCAC	2.31	2.25	2.22	2.63
LCAH	2.62	2.30	2.34	2.80

For other statistics see Tables 27 , 29 and 31 .
Refer to text for explanation of abbreviations.

TABLE 27

Sample statistics of male and female Tadarida petersoni

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	14	33.79	0.17	32.60-34.60	23	33.38	0.12	32.30-34.10
3MET	14	35.22	0.21	33.70-36.80	23	34.85	0.16	33.70-37.10
3M1P	14	13.02	0.13	12.10-13.60	23	12.72	0.08	12.00-13.40
3M2P	14	12.55	0.11	11.70-13.20	23	12.13	0.10	11.30-13.25
4MET	14	33.33	0.10	32.00-35.80	23	33.15	0.22	29.20-35.05
4M1P	14	10.74	0.16	10.00-12.40	23	10.32	0.08	9.60-11.00
4M2P	14	8.04	0.34	6.40-10.20	23	7.10	0.16	6.00- 8.70
5MET	14	22.59	0.18	21.50-24.30	23	21.96	0.15	20.00-23.00
5M1P	14	9.15	0.11	8.60- 9.95	23	8.78	0.10	7.70- 9.90
5M2P	14	2.85	0.05	2.60- 3.20	23	2.83	0.04	2.40- 3.50
GSLN	14	17.08	0.08	16.40-17.44	23	16.65	0.08	15.80-17.40
CDIN	14	15.94	0.09	15.20-16.35	23	15.47	0.08	14.95-16.55
PALL	14	6.86	0.06	6.30- 7.20	23	6.56	0.04	6.20- 6.95
ZYGO	14	10.97	0.07	10.45-11.25	23	10.52	0.05	10.15-10.95
MAST	14	10.22	0.08	9.65-11.05	23	9.92	0.04	9.60-10.40
BBCS	14	8.76	0.05	8.40- 9.10	23	8.59	0.04	8.30- 8.90
HBCS	14	5.65	0.03	5.40- 5.90	23	5.53	0.04	5.20- 6.00
ROWL	14	5.76	0.08	5.35- 6.25	23	5.42	0.04	5.00- 5.70
IOWA	14	4.25	0.06	3.90- 4.70	23	4.12	0.05	3.65- 4.60
POCN	14	3.46	0.03	3.25- 3.70	23	3.41	0.03	3.20- 3.70
M3M3	14	7.41	0.03	7.25- 7.60	23	7.29	0.03	7.10- 7.65
CANM	14	5.99	0.04	5.70- 6.25	23	5.90	0.03	5.65- 6.25
CANC	14	4.67	0.06	4.00- 4.90	23	4.22	0.03	3.95- 4.50
CANH	14	3.09	0.07	2.40- 3.40	23	2.47	0.03	2.20- 2.75
WBSP	14	0.76	0.02	0.65- 0.90	23	0.75	0.02	0.60- 0.90
LBSP	14	1.18	0.01	1.10- 1.25	23	1.14	0.02	0.95- 1.30
CNIL	14	11.48	0.07	10.75-11.80	23	11.10	0.06	10.30-11.70
GMLN	14	12.23	0.06	11.80-12.60	23	11.89	0.05	11.50-12.55
LCAM	14	6.64	0.04	6.35- 6.90	23	6.42	0.03	6.05- 6.70
LCAC	14	2.22	0.03	2.10- 2.35	23	2.04	0.02	1.80- 2.20
LCAH	14	2.34	0.04	1.85- 2.50	23	1.91	0.02	1.75- 2.15

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Fig. 50

Dorsal and ventral views of:

A. T. nanula

B. T. petersoni

C. T. brachyptera.

Fig. 50

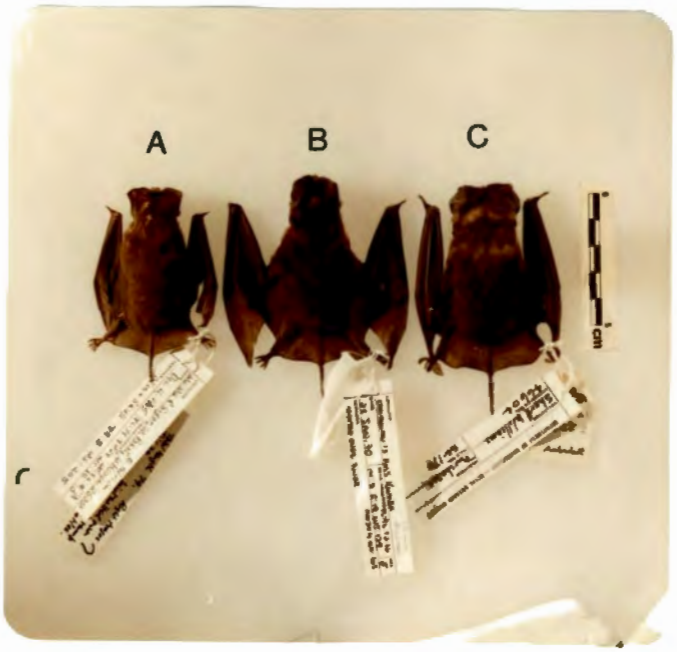


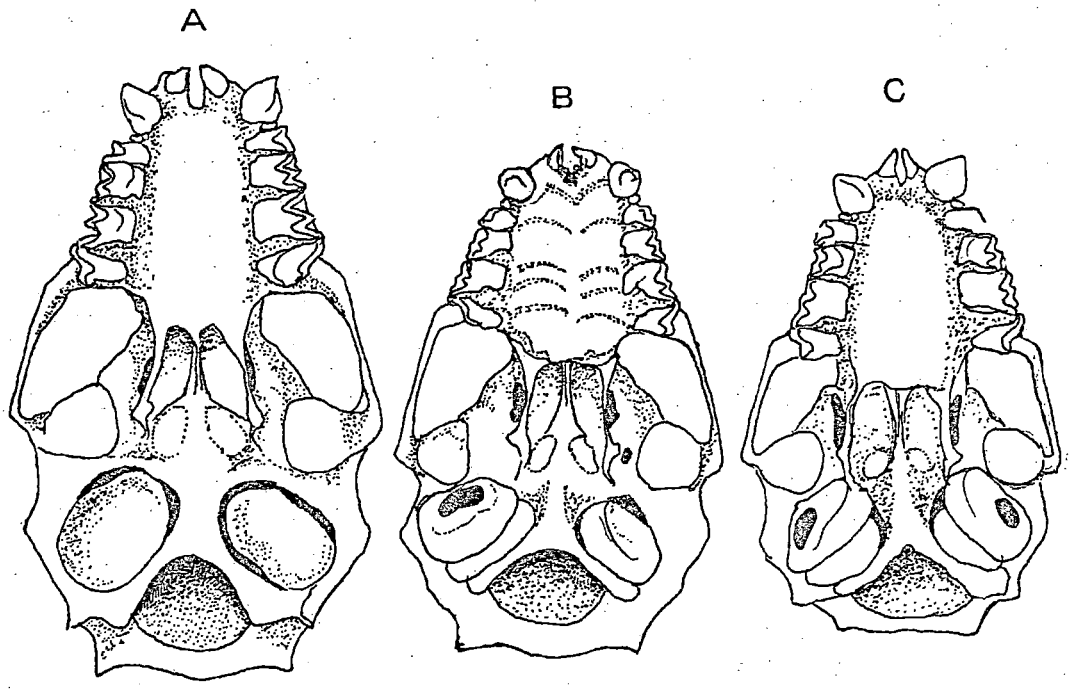
Fig. 51

Ventral(A) and dorsal(*A) views of T. brachyptera skull.

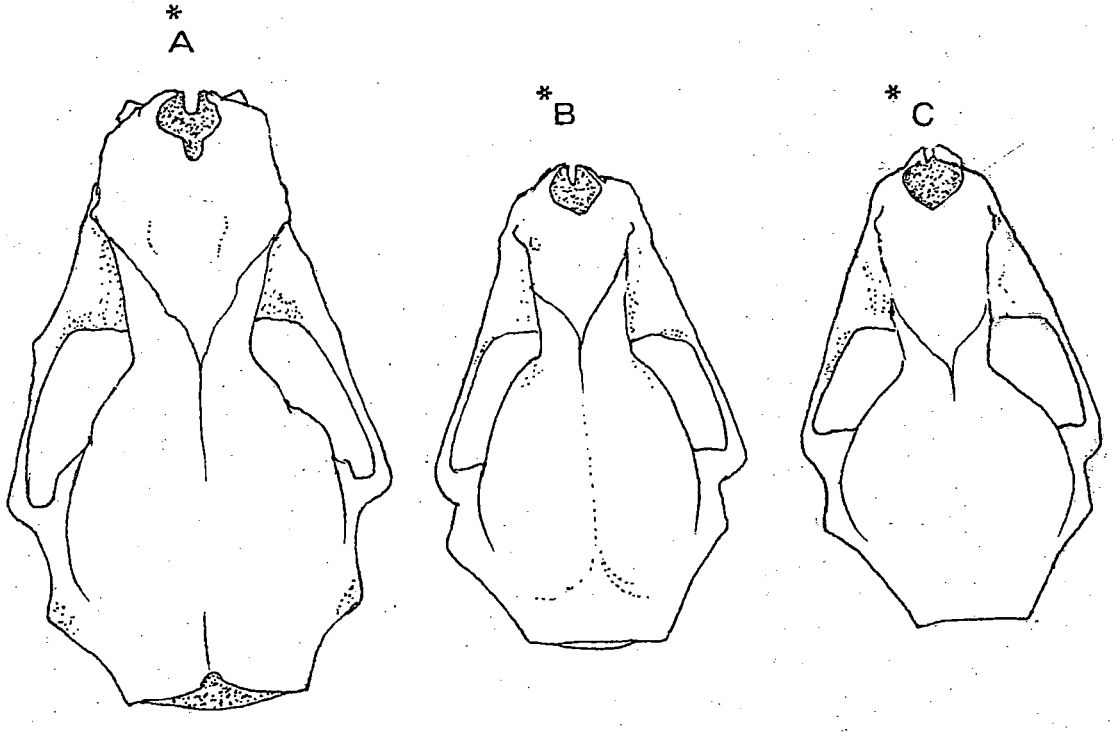
Ventral(B) and dorsal(*B) views of T. petersoni skull.

Ventral(C) and dorsal(*C) views of T. nanula skull.

Fig. 51



10 mm.

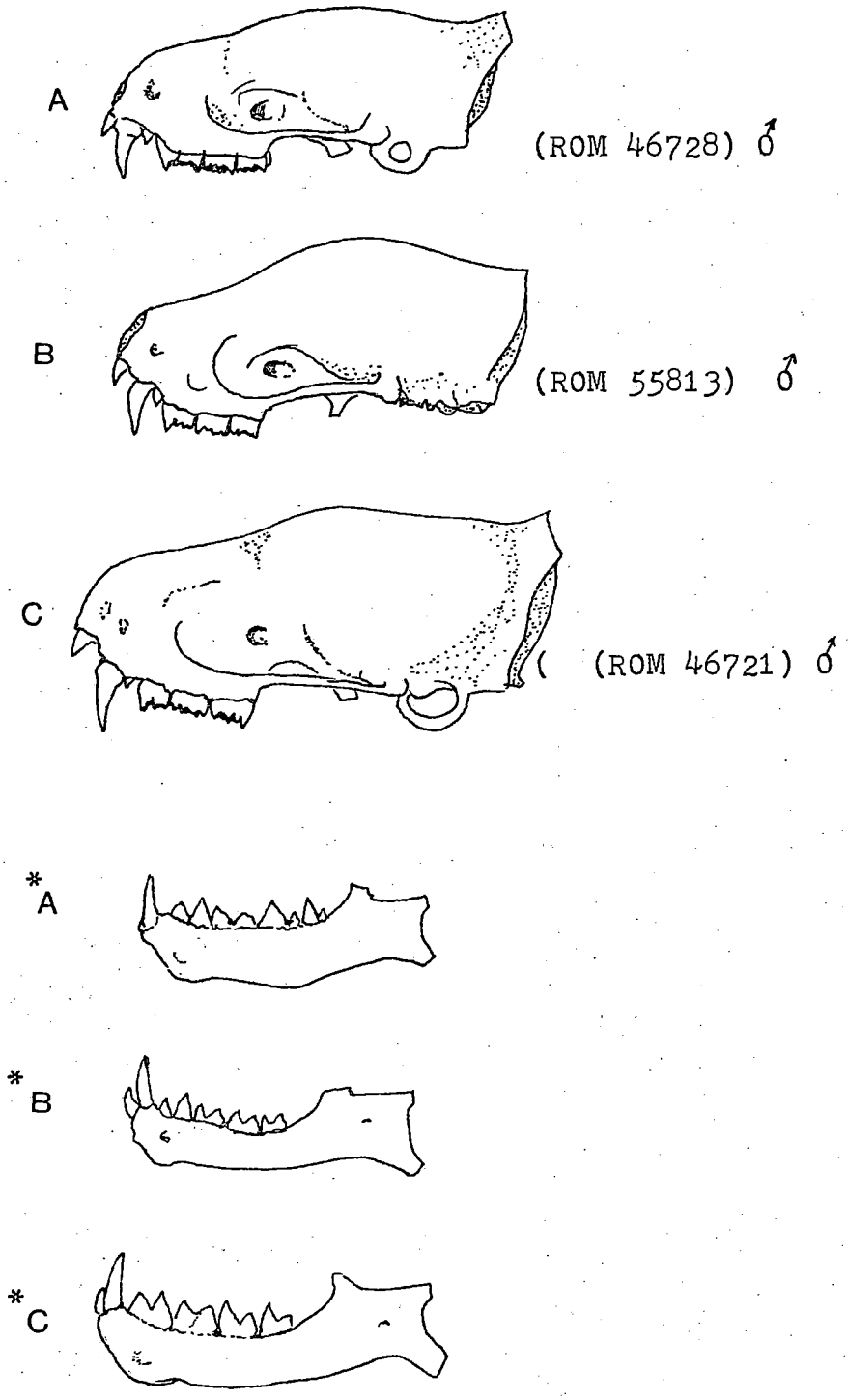


♂ (ROM 46721) ♂ (ROM 55813) ♂ (ROM 46728)

Fig. 52

Lateral views of (A) skull and (*A) mandible of T. nanula.
Lateral views of (B) skull and (*B) mandible of T. petersoni.
Lateral views of (C) skull and (*C) mandible of T. brachyptera.

Fig. 52



Tadarida (Mops) brachyptera (Peters)

Dysopes brachypterus Peters, 1852, Reise nach Mossambique. Zoologie. 1. Säugethiere. Berlin., p. 59. Island of Mozambique.

Nyctinomus brachypterus Dobson, 1876, Proc. Zool. Soc. Lond. p. 722. Sierra Leone.

Nyctinomus leonis Thomas, 1908, Ann. Mag. Nat. Hist. Ser. 8 (2): 373. Freetown, Sierra Leone.

Nyctinomus ochraceus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 445. Medje, Zaire.

Mops brachypterus G. M. Allen, 1939, Checklist of African Mammals. Bull. Mus. Comp. Zool. 83: 107.

Tadarida (Mops) brachyptera Swynnerton and Hayman, 1951, J. E. Af . Nat. Hist. Soc. 20(90): 296.

Tadarida (Mops) leonis Rosevear, 1953, Checklist and Atlas of Nigerian Mammals: 90.

Tadarida (Xiphonycteris) leonis leonis Koopman, 1975, Bull. Amer. Mus. Nat. Hist. 154(4): 420.

Tadarida (Xiphonycteris) leonis ochraceus Koopman, 1975, Bull. Amer. Mus. Nat. Hist. 154(4): 420.

Holotype

In Berlin Museum (lost).

Neotype

Male, adult, skin and skull, ROM 46721, from Budongo Forest, western Uganda, collected on June 24, 1968, by T. M. Shortt and J. Williams (field number SG 301).

Specimens Examined (125)

Cameroun: 67 km. W. Ayos 1 ♂, 1 ♀ (ROM); Lolodorf 1 ♂ (MCZ); E. Obula 1 ♀ (AMNH); Sounou River, 6 km. W. Mengeume, 1 ♂, 1 ♀ (ROM).

Central African Republic: 10 km. N. M'Baiki 2 ♂♂, 1 ♀ (CM)

Ghana: Ghiriso, Ashanti Region, 3 ♂♂, 6 ♀♀ (USNM); Doyum, Eastern Region, Accra Plains, 22 ♂♂, 26 ♀♀ (USNM): lekelbi, Volta Region, 3 ♀♀ (USNM); 55 km. W. Prestea, 7 ♀♀ (USNM); Yabrasso, Guinea Woodland, 1 ♂, 7 ♀♀ (USNM).

Sierra Leone: Freetown 1 ♂ (BMNH); 5 ♂♂, 6 ♀♀ (ROM).

Uganda: Sonso River, Budongo Forest, 1 ♂ (LCAM); 5 ♂♂, 4 ♀♀ (ROM).

Zaire: Medje, 4 ♂♂, 14 ♀♀ (AMNH); Panga 1 ♀ (AMNH).

Distribution

Sierra Leone, Ghana, Nigeria, Equatorial Guinea, Cameroun, Zaire, Uganda, Kenya, Zanzibar and Mozambique.

Description of Neotype

Dorsal colouration Mummy Brown hairs with white basal band (variable in other specimens, Russet or Cinnamon-Brown), extending to the posterolateral sides of the head; pelage colour on throat, chest and abdomen Pale Buff (variable in other specimens from White to Warm Buff and Ochraceous-Orange); pelage of humerus dorsally Mummy Brown; Dresden Brown ventrolaterally along the insertion of the endopatagium to the base of humerus and the femur. Dorsally and ventrally hair extends to the endopatagium. Dorsally hair short (about 3.5 mm); posterior to the band of tissue joining the two ears a thick mass of long Mummy Brown hair (about 6.0 mm) long; tragus small; antitragus quadrate as wide as long; lips wrinkled. Uropatagium and wing membranes Sepia.

First upper premolar small, internal to toothrow and filling up the space between the canine and the second premolar, upper incisors parallel, separated by anterior palatal emargination that extends posteriorly; third commissure on the last upper molar (M^3) reduced much shorter than second; basisphenoid pits deep, extend forward in an oval shape; basioccipital region well developed, curving dorsally and forming a helmet; strong mandible with well developed coronoid process; first lower premolar is slightly smaller than second but much wider at the base; lower incisors bifid and filling the space between the canines.

Measurements of the Neotype

Total length, 103 mm; tail length 33 mm; hind foot, 10 mm; ear, 20 mm (for other measurements see Tables 28 and 29).

Comparison

A comparison of skull measurements of the neotype (ROM 46721) and the holotype (measured from drawings) is given in Table 28.

Table 28

Measurements of Neotype (ROM 46721) and the Holotype of T. brachyptera. See text for character abbreviations.

Character	Neotype ROM 46721	Peters (1852) Holotype	
FOAR	39.70	38.8*	37.0**
3MET	41.30	38.3*	36.5**
3M1P	16.0	15.5*	15.0**
3M2P	15.4	14.5*	14.0**
4MET	39.80	37.9*	35.0**
4M1P	12.70	12.3*	12.0**
4M2P	9.50	9.0*	8.5**
5MET	26.50	24.3*	22.0**
5M1P	10.70	9.6*	9.0**
5M2P	3.20	3.2*	3.25**
GSLN	20.20	20.9*	21.50**
CDIN	18.50	18.95*	
PALL	8.10	-	
ZYGO	12.20	12.50*	
MAST	11.45	11.65*	
BBCS	9.90	10.00*	
HBCS	5.75	-	
ROWL	7.10	--	
IOWA	5.85	6.00*	
POCN	3.80	-	
M3M3	8.30	-	
CANM	6.90	-	
CANC	5.60	6.40*	
CANH	3.70	3.55*	
WBSP	0.80	-	
LBSP	1.40	-	
CNIL	13.40	13.70*	
GMLN	13.90	14.05*	
LCAM	7.70	8.20*	
LCAC	2.60	2.90*	
LCAH	2.85	3.10*	

* From Figure drawings.

** Measured by Peters.

TABLE 29

Sample Statistics of male and female Tadarida brachyptera.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	45	36.93	0.16	35.00-39.90	74	36.62	0.15	35.00-39.75
3MET	45	38.69	0.20	36.80-41.95	74	38.31	0.15	36.10-41.10
3M1P	45	14.89	0.10	13.70-16.60	74	14.60	0.07	13.30-16.20
3M2P	45	14.70	0.10	13.10-16.25	74	14.25	0.08	12.50-15.90
4MET	45	37.20	0.18	35.60-40.50	74	36.90	0.15	34.30-39.30
4M1P	45	11.95	0.08	10.90-13.10	74	11.79	0.06	10.90-12.80
4M2P	45	8.40	0.11	7.30- 9.90	74	8.48	0.09	7.10-10.30
5MET	45	25.08	0.14	23.40-27.45	74	24.72	0.11	22.80-26.80
5M1P	45	9.85	0.10	8.80-11.60	74	9.68	0.08	8.00-11.80
5M2P	45	3.37	0.05	2.80- 4.40	74	3.21	0.04	2.70- 4.10
GSLN	45	19.17	0.08	18.20-20.60	74	18.31	0.05	17.20-19.85
CDIN	45	17.60	0.08	16.50-18.70	74	16.81	0.06	15.70-18.25
PALL	45	7.68	0.04	6.85- 8.10	74	7.25	0.03	6.80- 7.85
ZYGO	45	12.03	0.06	11.15-13.00	74	11.51	0.04	10.80-12.35
MAST	45	10.98	0.05	10.10-11.70	74	10.67	0.03	10.00-11.25
BBCS	45	9.54	0.04	9.00-10.20	74	9.21	0.03	8.80- 9.80
HBCS	45	5.86	0.04	5.40- 6.85	74	5.70	0.03	5.15- 6.20
ROWL	45	6.72	0.04	6.20- 7.20	74	6.30	0.03	5.80- 6.90
IOWA	45	5.32	0.04	4.60- 6.30	74	5.07	0.04	4.50- 6.45
POCN	45	3.82	0.03	3.40- 4.20	74	3.78	0.02	3.35- 4.15
M3M3	45	8.04	0.05	7.35- 8.75	74	7.86	0.04	7.30- 8.60
CANM	45	6.78	0.03	6.40- 7.40	74	6.45	0.03	6.00- 7.30
CANC	45	5.35	0.04	4.75- 6.10	74	4.80	0.04	4.30- 6.20
CANH	45	3.54	0.04	2.45- 4.15	74	2.82	0.03	2.45- 4.30
WBSP	45	0.90	0.02	0.75- 1.20	74	0.89	0.01	0.70- 1.20
LBSP	45	1.32	0.01	1.00- 1.50	74	1.29	0.01	1.10- 1.50
CNIL	45	12.98	0.05	12.20-14.05	74	12.24	0.14	11.00-13.35
GMLN	45	13.62	0.05	12.75-14.60	74	12.98	0.05	11.75-14.10
LCAM	45	7.48	0.04	7.00- 8.35	74	7.16	0.08	6.10- 8.75
LCAC	45	2.63	0.03	2.25- 3.10	74	2.38	0.06	2.00- 3.80
LCAH	45	2.80	0.02	2.55- 3.30	74	2.21	0.01	1.95- 2.50

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (Mops) spurrelli (Dollman)

Xiphonycteris spurrelli Dollman, 1911, Ann. Mag. Nat. Hist. (8): 210. Bibianaha, 96 km. west of Kumasi, Ghana.

Tadarida (Xiphonycteris) spurrelli Koopman, 1975, Bull. Amer. Mus. Nat. Hist., 154(4): 420.

Holotype

Adult ♂ (BMNH 11.1.11.1), collected on December 8th, 1910, by Dr. H. G. F. Spurrel at Bibianaha, 96 km. west of Kumasi, Ghana.

Distribution

Ivory Coast, Ghana, Cameroun, Central African Republic, Equatorial Guinea.

Specimens Examined (131)

Cameroun: 67 km. W. Ayos, 13 ♂♂, 10 ♀♀ (ROM); 7 km. N. Eseka 1 ♀ (AMNH): 15 km. S. Kumba 6 ♂♂, 4 ♀♀ (ROM); Mawut Village 1 ♂, 4 ♀♀ (ROM); 30 km. E. Nanga Emboko, 1 ♂, 1 ♀ (AMNH): N. Ntui, 2 ♀♀ (ROM); 4 km. S. E. Obula, 6 ♂♂, 10 ♀♀ (ROM); 82 km. N. E. Obula, 1 ♀ (AMNH): E. Okola, 1 ♂, 1 ♀ (AMNH).

Central African Republic: 10 km. N. M'Baiki, 4 ♂♂, 1 ♀ (CM).

Equatorial Guinea: Fernando Po, 1 ♀ (skull only) (SMF); Rio Muni, 2 ♂♂ (USNM).

Ivory Coast: Banco Forest, 1 ♀ (AMNH), 2 ♀♀ (USNM); Ehania, 1 ♂, 3 ♀♀ (USNM).

Ghana: Jukwa, Central Region, 7 ♀♀ (USNM); N.W. Kade, 2 ♂♂, 5 ♀♀ (ROM), 1 ♂ (USNM); Lekelbi, 20 ♂♂, 20 ♀♀ (USNM); W. Prestea, 1 ♀ (USNM).

Measurments

As shown in Table 30.

Remarks

The Spurrell free-tailed bat is characterized by large upper and lower canines with huge cingula. In males, the lower canines often meet over the incisors which are reduced to minute teeth. However, the number of lower incisors is variable and appears to be related to age. In older individuals, lower incisors may sometimes be absent (pers. obser.).

T. spurrelli is the smallest species of the subgenus Mops. Externally it resembles T. nanula but smaller. The colour of the dorsum is uniform Cinnamon Brown, whereas the venter is characterized by an Ochraceous-Tawny colour on the throat and a unicolourus grey hair on chest and abdomen. Specimens of T. spurrelli have been misidentified occassionally at some institutions as T. nanula. For example, specimen (AMNH 239412) identified as T. n. calabarensis (Fig. 53) and all the series of specimens (USNM 412218 -- 412225, 424901 -- 424936, 450009, 450017, 450018 and 450100) identified as T. nanula are T. spurrelli.

Fig. 53

Dorsal (A) and ventral (A*) views of T. spurrelli from Cameroun (AMNH 241081) compared to (AMNH 239413) from Ivory Coast , incorrectly identified as T. nanula calabaresis (B) dorsal (B*) ventral views.

Fig. 53

A B

*A *B

TABLE 30

Sample statistics of male and female Tadarida spurrelli.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	54	28.33	0.10	26.70-30.00	73	27.96	0.10	26.60-30.00
3MET	54	29.50	0.07	28.50-30.90	73	29.04	0.08	27.30-30.90
3M1P	54	10.77	0.05	10.00-11.85	73	10.53	0.05	9.00-11.30
3M2P	54	10.59	0.06	9.60-11.30	73	10.30	0.06	8.40-11.40
4MET	54	28.46	0.08	27.10-30.00	73	27.30	0.11	22.30-29.60
4M1P	54	8.96	0.06	7.85-10.00	73	8.83	0.06	7.90- 9.90
4M2P	54	6.82	0.08	5.20- 8.10	73	6.73	0.07	5.50- 7.90
5MET	54	19.81	0.10	18.90-23.60	73	19.32	0.06	18.00-20.50
5M1P	54	7.10	0.05	6.50- 7.80	73	6.94	0.05	5.90- 8.10
5M2P	54	2.52	0.04	2.00- 3.30	73	2.44	0.03	1.90- 3.50
GSLN	54	16.04	0.06	14.50-16.80	73	15.27	0.04	14.00-16.10
CDIN	54	14.80	0.06	13.80-15.85	73	14.06	0.04	13.00-15.60
PALL	54	6.67	0.04	5.95- 7.30	73	6.07	0.03	5.15- 6.60
ZYGO	54	10.24	0.05	9.40-11.05	73	9.76	0.03	9.10-10.40
MAST	54	9.57	0.03	9.00-10.00	73	9.31	0.02	8.65- 9.95
BBCS	54	8.11	0.03	7.65- 8.65	73	7.79	0.03	7.10- 8.32
HBCS	54	2.87	0.03	4.25- 5.80	73	4.71	0.04	4.10- 5.10
ROWL	54	5.70	0.03	5.15- 6.10	73	5.27	0.02	4.80- 5.70
IOWA	54	4.70	0.04	4.10- 5.55	73	4.35	0.03	3.75- 5.00
POCN	54	3.27	0.01	3.00- 3.50	73	3.25	0.01	3.00- 3.50
M3M3	54	7.08	0.03	6.55- 7.50	73	6.87	0.02	6.40- 7.25
CANM	54	6.17	0.03	5.60- 6.60	73	5.70	0.02	5.20- 6.10
CANC	54	4.70	0.03	4.15- 5.10	73	3.93	0.02	3.60- 4.70
CANH	54	3.18	0.02	2.90- 3.70	73	2.33	0.02	2.00- 2.80
WBSP	54	0.80	0.02	0.60- 1.05	73	0.79	0.01	0.60- 1.00
LBSP	54	0.82	0.01	0.65- 1.00	73	0.84	0.01	0.70- 1.00
CNIL	54	11.26	0.04	10.50-12.10	73	10.52	0.03	9.60-11.10
GMLN	54	11.72	0.05	10.70-12.70	73	11.00	0.04	10.20-11.68
LCAM	54	6.89	0.03	6.20- 7.40	73	6.27	0.02	5.75- 6.75
LCAC	54	2.39	0.02	2.05- 2.75	73	1.80	0.01	1.32- 2.10
LCAH	54	2.76	0.06	2.25- 2.80	73	1.81	0.02	1.50- 2.50

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (*Mops*) *nanula* (J. A. Allen)

Mops (*Allomops*) *nanulus* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 477. Niangara, Zaire.

Mops nanulus G. M. Allen, 1939, Checklist of African Mammals. Bull. Mus. Comp. Zool., 83: 109.

Mops calabarensis Hayman, 1940, Trans. Zool. Soc., London, 24: 677. Ikotombo, near Calabar, Nigeria.

Tadarida (*Mops*) *calabarensis* Rosevear, 1953, Checklist and Atlas of Nigerian Mammals: 90.

Tadarida (*Mops*) *nanulus* Rosevear, 1953, Checklist and Atlas of Nigerian Mammals: 90.

Tadarida (*Xiphonycteris*) *nanula* Koopman, 1975, Bull. Amer. Mus. Nat. Hist., 154(4): 420.

Holotype

Adult ♂ (AMNH 48864), collected by Herbert Lang and J. P. Chapin at Niangara, Zaire, on December 12, 1910.

Distribution

Forests of Sierra Leone, Liberia, Ghana, Benin, Nigeria, Cameroun, Zaire, Sudan.

Specimens Examined (96)

Benin: Nikki, Borgou Region 5 ♀♀ (USNM);

Cameroun: Idenau, 50 km. W. of Bota, 11 ♂♂, 8 ♀♀ (ROM); Njombo River, 67 km. W. of Ayos, 3 ♀♀ (ROM).

Kenya: Wei Wei River, Sigor, W. Pokot, 7 ♂♂, 16 ♀♀ (ROM), 1 ♀ (SMF).

Sudan: Yambio, 1 ♂, 4 ♀♀ (ROM).

Uganda: Sonso River, Budongo Forest, 8 ♂♂, 29 ♀♀ (ROM).

Zaire: Niangara, 2 ♂♂, 1 ♀ (AMNH).

Measurements

As shown in Table 31.

Comments

This species exhibits a wide range of pelage colour. Rosevear (1965: 344) described colour variation in 13 specimens from Luluabourg, Zaire, and stated that: "the fur of the back may range from a fairly bright orange-brown to blackish-brown; and that the underside may be entirely pale red-brown, or with a central area, variable in extent of yellowish-brown, grey or white, the flanks ranging from brown to sepia."

In 37 specimens from the Budongo Forest, Uganda, I also observed wide range of colour variation (Fig. 43). Dorsal colouration varied from Army Brown, Bone Brown, through Cinnamon, Bister and Snuff Brown, whereas ventral pelage colouration varied from White and Pale Drab-Gray to

Antimony Yellow, with Prout's Brown on the ventrolateral surfaces. T. nanula is larger than T. spurrelli, and the two species are the smallest in the subgenus Mops.

TABLE 31

Sample statistics of male and female Tadarida nanula.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	29	30.25	0.13	28.40-31.10	67	29.34	0.10	27.90-31.00
3MET	29	31.08	0.16	29.30-32.20	67	30.41	0.09	29.15-32.50
3M1P	29	11.61	0.10	10.60-12.80	67	11.50	0.06	10.30-12.30
3M2P	29	11.29	0.10	10.60-12.70	67	11.01	0.07	9.20-12.10
4MET	29	30.08	0.25	26.90-31.05	67	29.21	0.09	27.00-30.60
4M1P	29	9.22	0.21	8.99-10.30	67	9.33	0.05	8.30-10.20
4M2P	29	7.69	0.27	6.78- 9.30	67	7.86	0.07	6.70- 9.00
5MET	29	20.41	0.12	18.90-21.80	67	20.09	0.08	17.90-21.80
5M1P	29	7.74	0.08	6.40- 8.50	67	7.62	0.07	6.10- 8.90
5M2P	29	2.79	0.07	2.30- 3.80	67	2.86	0.04	2.10- 3.50
GSLN	29	16.52	0.10	15.10-17.45	67	15.79	0.04	15.00-16.65
CDIN	29	15.43	0.08	14.60-16.10	67	14.65	0.04	13.90-15.35
PALL	29	6.74	0.06	6.20- 7.30	67	6.33	0.03	5.90- 6.80
ZYGO	29	10.44	0.06	9.90-11.05	67	10.01	0.03	9.50-10.50
MAST	29	9.90	0.05	9.30-10.45	67	9.65	0.03	9.00-10.20
BBCS	29	8.34	0.04	7.75- 8.90	67	8.18	0.04	7.35- 9.70
HBCS	29	4.77	0.05	4.40- 5.30	67	4.76	0.02	4.35- 5.00
ROWL	29	5.96	0.05	5.35- 6.60	67	5.45	0.03	4.60- 6.05
IOWA	29	4.52	0.03	4.10-5.00	67	4.26	0.05	3.70- 4.80
POCN	29	3.53	0.04	3.25- 3.80	67	3.43	0.02	3.05- 3.85
M3M3	29	7.38	0.04	6.95- 7.70	67	7.14	0.02	6.70- 7.55
CANM	29	6.11	0.05	5.75- 6.60	67	5.82	0.02	5.30- 6.25
CANC	29	4.74	0.07	4.20- 5.20	67	4.11	0.02	3.50- 4.45
CANH	29	3.26	0.06	2.50- 3.70	67	2.50	0.02	1.90- 2.90
WBSP	29	0.96	0.02	0.70- 1.15	67	0.96	0.01	0.70- 1.05
LBSP	29	0.94	0.01	0.80- 1.10	67	0.95	0.01	0.70- 1.10
CNIL	29	11.47	0.03	10.80-12.10	67	10.82	0.04	9.90-11.40
GMLN	29	11.89	0.03	10.90-12.50	67	11.25	0.04	10.40-11.75
LCAM	29	6.88	0.04	6.50- 7.25	67	6.42	0.02	6.00- 6.80
LCAC	29	2.31	0.03	1.95- 2.65	67	1.94	0.01	1.70- 2.15
LCAH	29	2.62	0.04	1.95- 2.90	67	1.88	0.02	1.20- 2.10

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (*Mops*) *thersites* (Thomas)

Nyctinomus thersites Thomas, 1903, Ann. Mag. Nat. Hist., 12(7): 634. Efulen, Cameroun.

Mops (*Allomops*) *occipitalis* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 474.

Mops brachypterus De Beaux, 1922, Ann. Mus. Civ. Stor. Nat. Genova, 3(9): 364-373.

Mops occipitalis G. M. Allen, 1939, Checklist of African Mammals, Bull. Mus. Comp. Zool., 83: 109.

Mops thersites G. M. Allen, 1939, Checklist of African Mammals, Bull. Mus. Comp. Zool., 83: 108.

Tadarida (*Mops*) *thersites* Rosevear, 1953, Checklist and Atlas of Nigerian Mammals: 90.

Tadarida (*Xiphonycteris*) *thersites* Koopman, 1975, Bull. Amer. Mus. Nat. Hist., 154(4): 420.

Holotype

Adult ♂ (BMNH 4.2.8.4.) collected by G. L. Bates from Efulen, Cameroun.

Distribution

Forest zones from Sierra Leone east through Liberia, Ivory Coast, Ghana, Togo, Nigeria, Cameroun, Zaire, Uganda.

Specimens Examined (136)

Cameroun: Bertua, 1 ♂ (AMNH); 2 ♀♀ (ROM); Bamenda, 3 ♀♀ (ROM); Eseka, 3 ♂♂, 4 ♀♀ (AMNH); 4 ♀♀ (ROM); Likomba, N. Tiko, 5 ♂♂, 5 ♀♀ (ROM); Nanga Emboko, 1 ♀ (AMNH); 2 ♂♂, 1 ♀ (ROM).

Ghana: 12 km. N. E. Kade, 11 ♂♂, 7 ♀♀ (ROM); W. Prestea, 8 ♂♂, 5 ♀♀ (USNM).

Ivory Coast: Adiapodoume, 3 ♂♂ (USNM); Banco Forest, 15 ♀♀ (USNM); 15 km. N. Lakota, Guebona, 1 ♂, 4 ♀♀ (AMNH).

Liberia: Tars Twon, 3 ♂♂, 1 ♀ (USNM).

Togo: Ezime, 5 ♀♀ (USNM).

Uganda: Bugala, 1 ♀ (AMNH); Buganda, Mangu District, Kabanyolo, 10 km. N. Kampala, 3 ♂♂, 3 ♀♀ (CUMZ); Budongo Forest, 1 ♂ (AMNH); 12 ♂♂, 11 ♀♀ (ROM).

Zaire: Luluabourg, 1 ♂ (AMNH); Medje, 4 ♂♂, 1 ♀ (AMNH).

Measurements

As shown in Table 32.

Comments

T. thersites, commonly known as the Railer bat has been confused with T. leonis (=brachyptera) from West Africa. Rosevear (1965) suggested that the two species might be conspecific since sometimes they occupy the same

roosting sites. T. thersites is morphologically similar to but slightly larger than T. brachyptera. The most distinguishing character is the nude posterior dorsolateral surfaces and the uniform Rust Brown colour of the ventral side of T. thersites. In T. brachyptera, the posterior dorsolateral surfaces are never nude, and the colour of the venter varies from Ochraceous-Orange to White, but is never brown. The basisphenoid pits of T. thersites are round, clearly defined, and the septum between them is wide. The third commissure on the last upper molar is partially reduced.

TABLE 32

Sample statistics of male and female Tadarida thersites.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	66	38.42	0.19	35.40-42.00	77	38.30	0.14	35.20-41.50
3MET	66	40.14	0.16	36.80-42.00	77	39.90	0.13	36.20-42.70
3M1P	66	16.49	0.08	15.00-17.70	77	16.34	0.06	14.80-17.40
3M2P	66	15.77	0.10	12.50-17.50	77	15.67	0.08	14.10-16.90
4MET	66	38.57	0.16	35.90-41.50	77	38.25	0.13	35.20-41.20
4M1P	66	13.59	0.08	11.90-14.90	77	13.41	0.06	12.40-14.70
4M2P	66	10.80	0.11	7.80-13.05	77	10.88	0.08	9.00-12.70
5MET	66	26.34	0.14	23.30-28.40	77	26.11	0.11	23.50-28.30
5M1P	66	10.60	0.06	9.40-11.60	77	10.35	0.05	9.00-11.20
5M2P	66	3.41	0.04	2.20- 4.20	77	3.29	0.03	2.50- 4.10
GSLN	66	19.39	0.07	17.70-20.55	77	18.52	0.09	17.90-19.80
CDIN	66	17.91	0.06	16.55-18.85	77	17.16	0.05	15.70-18.00
PALL	66	7.85	0.04	6.85- 8.40	77	7.44	0.03	6.80- 8.00
ZYGO	66	12.21	0.06	11.00-13.15	77	11.71	0.04	10.90-12.40
MAST	66	11.30	0.05	10.25-12.00	77	10.99	0.03	10.15-11.65
BBCS	66	9.70	0.03	9.20-10.35	77	9.53	0.03	8.85-10.10
HBCS	66	5.86	0.03	5.35- 6.70	77	5.75	0.02	5.30- 6.30
ROWL	66	6.81	0.04	5.85- 7.35	77	6.42	0.03	5.10- 7.10
IOWA	66	5.37	0.04	4.60- 6.10	77	5.20	0.03	4.65- 5.80
POCN	66	3.99	0.02	3.55- 4.40	77	3.94	0.02	2.90- 4.30
M3M3	66	8.27	0.03	7.60- 8.80	77	8.10	0.03	6.40- 8.60
CANM	66	6.79	0.03	6.20- 7.30	77	6.58	0.03	4.55- 7.00
CANC	66	5.48	0.04	4.70- 6.05	77	4.99	0.03	4.40- 5.60
CANH	66	3.61	0.03	2.50- 4.00	77	2.88	0.03	2.40- 3.75
WBSP	66	1.28	0.01	1.00- 1.45	77	1.27	0.01	1.10- 1.40
LBSP	66	0.83	0.01	0.65- 1.05	77	0.80	0.01	0.65- 1.05
CNIL	66	13.38	0.05	12.00-14.25	77	12.84	0.02	11.50-13.80
GMLN	66	14.14	0.04	12.80-14.95	77	13.49	0.04	12.20-14.40
LCAM	66	7.55	0.03	6.65- 8.10	77	7.26	0.03	6.75- 8.00
LCAC	66	2.75	0.02	2.35- 3.05	77	2.44	0.02	2.05- 2.95
LCAH	66	2.83	0.03	2.10- 3.20	77	2.17	0.02	1.80- 2.85

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (*Mops*) *demonstrator* (Thomas)

Nyctinomus demonstrator Thomas, 1903, Ann. Mag. Nat. Hist., (7)12: 501. Mangala, Equatoria Province, Sudan.

Chaerephon emini G. M. Allen, 1914, Bull. Mus. Comp. Zool. 58: 352. Aradeiba, Sudan.

Chaerephon bivittatus G. M. Allen, 1914, Bull. Mus. Comp. Zool., 58: 352. EL Garef (=EL-Gadarif), Sudan.

Mops (*Allomops*) *faradjuis* J. A. Allen, 1917, Bull. Amer. Nat. Hist., 37: 476. Faradje, Oriental Province, Zaire.

Mops demonstrator G. M. Allen, 1939, Checklist of African Mammals. Bull. Mus. Comp. Zool., 83: 107.

Tadarida (*Mops*) *demonstrator* Koopman, 1965, Amer. Mus. Novitates, 2219: 29.

Holotype

Adult ♂ (BMNH 2.7.4.3) collected by W. L. S. Loat at Mangala, north of Gondokoro, Sudan.

Distribution

Sudan, Uganda, Kenya, Zaire and possibly West Africa (according to Kock, 1969b).

Specimens Examined (7)

Kenya: Kisumu, Nyanza, 3 ♂♂ (ROM).

Uganda: Acholi district, 2 ♀♀ (ROM); Murchison Falls, 1 ♂ (ROM); Waisoka River, Budongo Forest, 1 ♂ (ROM).

Measurements

As shown in Table 33.

Comments

This species is commonly known as the Mangala free-tailed bat. Although the species is mostly distributed in the south and southeastern Sudan, Uganda, Kenya and Zaire, Kock (1969b) suggested that it could occur in West Africa on the basis of similar vegetation zones. If so, Koopman (1975) considered that T. demonstrator must have been confused with T. condylura or other species. In Koopman's opinion T. demonstrator is most closely related to T. niveiventer which has a restricted range in southern Zaire, Rwanda, Central Angola, Zambia and southwestern Tanzania.

T. demonstrator is characterized by a scent gland at the base of the penis. It has a Mouse Gray colour on the dorsum, more blackish on the head; with Pale Gull Gray to Light Purplish Gray on the venter. The skull is low in profile and the brain case is small. The third commissure of the last upper molar is completely reduced as in T. spurrelli, T. nanula and T. midas. The basisphenoid pits are well defined and larger than those of T. condylura.

TABLE 33

Sample statistics of male and female Tadarida demonstrator.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	5	44.06	0.97	40.60-46.00	2	40.95	0.65	40.30-41.60
3MET	5	45.86	1.00	42.20-48.30	2	44.80	0.40	44.40-45.20
3M1P	5	18.00	0.31	16.90-18.60	2	17.95	0.45	17.50-18.40
3M2P	5	17.36	0.27	16.40-17.90	2	17.00	0.10	16.90-17.10
4MET	5	44.22	0.87	40.90-45.90	2	43.15	0.45	42.70-43.60
4M1P	5	15.16	0.33	14.10-15.90	2	14.65	0.15	14.50-14.80
4M2P	5	11.80	0.21	11.00-12.20	2	12.25	0.15	12.10-12.40
5MET	5	28.40	0.49	26.70-29.30	2	27.20	0.40	26.80-27.60
5M1P	5	12.54	0.19	12.00-13.00	2	12.10	0.30	11.80-12.40
5M2P	5	4.64	0.10	4.30- 4.90	2	4.60	0.30	4.30- 4.90
GSLN	5	21.04	0.39	19.90-21.70	2	19.75	0.25	19.50-20.00
CDIN	5	19.35	0.31	18.45-20.00	2	18.07	0.22	17.85-18.30
PALL	5	8.57	0.09	8.30- 8.75	2	8.00	0.00	--
ZYGO	5	12.94	0.25	12.30-13.55	2	12.32	0.38	11.95-12.70
MAST	5	11.62	0.21	11.10-12.10	2	11.07	0.22	10.85-11.30
BBCS	5	10.11	0.19	9.50-10.55	2	9.75	0.25	9.50-10.00
HBCS	5	6.24	0.13	5.90- 6.65	2	5.97	0.17	5.80- 6.15
ROWL	5	7.43	0.07	7.25- 7.60	2	6.93	0.07	6.85- 7.00
IOWA	5	6.06	0.12	5.75- 6.45	2	5.25	0.04	5.20- 5.30
POCN	5	4.04	0.06	3.90- 4.25	2	4.07	0.18	3.90- 4.25
M3M3	5	9.12	0.17	8.65- 9.45	2	8.57	0.32	8.25- 8.90
CANM	5	7.51	0.21	6.75- 7.95	2	7.13	0.02	7.10- 7.15
CANC	5	6.03	0.21	5.25- 6.40	2	5.43	0.18	5.25- 5.60
CANH	5	4.20	0.10	4.00- 4.50	2	3.27	0.12	3.15- 3.40
WBSP	5	0.81	0.04	0.75- 0.95	2	1.02	0.03	1.00- 1.05
LBSP	5	1.37	0.09	1.15- 1.70	2	1.43	0.12	1.30- 1.55
CNIL	5	14.54	0.26	13.65-15.05	2	13.70	0.05	13.65-13.75
GMLN	5	15.01	0.26	14.30-15.60	2	14.00	0.00	--
LCAM	5	8.46	0.17	7.95- 8.80	2	7.95	0.00	--
LCAC	5	2.91	0.06	2.70- 3.00	2	2.50	0.00	--
LCAH	5	3.25	0.06	3.10- 3.40	2	2.65	0.00	--

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (Mops) condylura (A. Smith)

Nyctinomus condylurus A. Smith, 1833, S. Afr. Quart. J., 2:54. Port Natal (=Durban), South Africa.

Nyctinomus "sp. nov." Peters, 1870, J. Sci. Math. Phys. e Nat. 3(1): 124. Quenza River, Angola.

Nyctinomus angolensis Gunther, 1871, Zool. Rec. for 1870: 8 Quenza River, Angola.

Mops (Allomops) osborni J. A. Allen, 1917, Bull. Amer. Mus. 37: 473. Kinshasa, Zaire.

Mops angolensis wonderi Sanborn, 1936, Zool. Ser., Field Mus. Nat. Hist., 20:114. Sotuba, 7 km. east of Bamako, Mali.

Mops angolensis angolensis G. M. Allen, 1939, Checklist of African Mammals, Bull. Mus. Comp. Zool., 83: 107.

Mops osborni occidentalis Monard, 1939, Archos Mus. Bocage, 10: 78. Mansoa, Guinea-Bissau.

Mops angolensis orientis G. M. Allen and A. Loveridge, 1942, Bull. Mus. Comp. Zool., 89: 166. Kitaya, Rovuma River, southeastern Tanzania.

Mops condylurus Roberts, 1951, The Mammals of South Africa, p. 97.

Tadarida (Mops) condylura Ellerman, Morrison-Scott and Hayman, 1953, Southern African Mammals, p. 69.

Holotype

Not known.

Distribution

From South Africa northward to Angola, Tanzania, Kenya, Zaire, Uganda, Sudan, Somalia and throughout West Africa as far west as Guinea and Gambia.

Specimens Examined (20)

Kenya: Athi River, 3 ♀♀ (ROM); Lake Baringo, 3 ♀♀ (ROM); Wangala, 10 ♂♂, 4 ♀♀ (ROM).

Measurements

As shown in Table 34.

Comments

This species, known as the Angola free-tailed bat, occupies a wide variety of habitats from the Sahel woodland to the evergreen rain-forest belt. It also shows wide range of colour variation. The colour on the dorsum varies from Army Brown to Balckish Brown. Ventral pelage is commonly White, but in some individuals it is Drab Gray on the throat and Hair Brown on the sides. Several subspecies were described and assigned to T. condylura, but the validity of these subspecies is doubtful.

The most distinguishing character in the skull of this species is the very large Lambdoid crest that projects posteriorly. The anterior upper premolar is very minute and is externally out of the toothrow; and in some specimens absent. Although the third commissure of the last upper molar is reduced, as in all members of the subgenus Mops, it is longer than in any other Mops. The basisphenoid pits are round and small and separated by a wide septum.

Whereas Hayman and Hill (1971) regard T. leucostigma from Madagascar to be allied to T. niveiventer, R. L. Peterson (pers. comm.) who examined many specimens, considers T. leucostigma to be closely related to T. condylura.

TABLE 34

Sample statistics of male and female Tadarida condylura.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	10	45.92	0.38	43.50-47.00	10	45.61	0.35	44.00-46.80
3MET	10	47.98	0.21	46.20-49.30	10	46.80	0.26	45.20-47.60
3M1P	10	21.77	0.23	21.00-22.90	10	20.98	0.21	20.10-22.00
3M2P	10	20.89	0.32	20.20-22.30	10	20.48	0.30	19.00-22.10
4MET	10	46.20	0.23	44.40-47.60	10	45.43	0.31	43.60-46.70
4M1P	10	17.74	0.24	16.70-18.90	10	17.37	0.29	16.00-18.30
4M2P	10	15.94	0.32	15.00-17.50	10	15.08	0.33	13.20-16.30
5MET	10	32.02	0.10	30.20-33.60	10	31.05	0.35	29.80-33.20
5M1P	10	12.98	0.07	12.60-13.70	10	12.74	0.16	11.80-13.20
5M2P	10	4.83	0.10	4.40- 5.20	10	4.81	0.13	4.00- 5.40
GSLN	10	21.41	0.10	20.90-21.90	10	20.42	0.17	19.70-21.15
CDIN	10	19.20	0.11	18.65-19.60	10	18.35	0.16	17.65-19.10
PALL	10	8.80	0.08	8.10- 9.30	10	8.36	0.13	7.80- 9.10
ZYGO	10	13.16	0.11	12.70-13.45	10	12.56	0.10	12.15-13.05
MAST	10	11.95	0.08	11.35-12.50	10	11.67	0.09	11.35-12.25
BBCS	10	10.56	0.17	10.20-10.90	10	10.36	0.05	10.15-10.65
HBCS	10	7.63	0.08	6.45- 8.15	10	6.97	0.14	6.30- 7.70
ROWL	10	7.58	0.08	7.350 8.00	10	7.20	0.10	6.80- 7.65
IOWA	10	6.84	0.05	6.50- 7.15	10	6.42	0.12	6.00- 6.90
POCN	10	4.49	0.07	4.30- 4.70	10	4.41	0.03	4.30- 4.60
M3M3	10	9.05	0.04	8.70- 9.35	10	8.80	0.07	8.55- 9.20
CANM	10	7.47	0.06	7.25- 7.65	10	7.16	0.06	6.90- 7.40
CANC	10	6.23	0.03	5.90- 6.50	10	5.62	0.03	5.50- 5.85
CANH	10	4.36	0.10	4.25- 4.50	10	3.53	0.07	3.20- 3.90
WBSP	10	1.61	0.03	1.50- 1.75	10	1.60	0.04	1.45- 1.85
LBSP	10	0.94	0.04	0.80- 1.15	10	0.93	0.02	0.85- 1.10
CNIL	10	14.56	0.10	14.00-15.00	10	13.78	0.11	13.30-14.40
GMLN	10	15.08	0.08	14.65-15.50	10	14.48	0.11	14.10-15.15
LCAM	10	8.35	0.06	8.00- 8.55	10	8.04	0.07	7.70- 8.40
LCAC	10	3.03	0.03	2.90- 3.20	10	2.79	0.04	2.65- 3.15
LCAH	10	3.40	0.04	3.25- 3.65	10	2.83	0.06	2.55- 3.05

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Tadarida (*Mops*) *congica* (J. A. Allen)

Mops congicus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 467. Medje, Zaire.

Tadarida (*Mops*) *congicus congicus* Koopman, 1965, Amer. Mus. Novitates, 2219: 29.

Tadarida (*Mops*) *congica* Peterson, 1972, Life Sci. Contr., Roy. Ont. Mus., 85: 10.

Holotype

An adult ♀ (AMNH 48893) collected by Herbert Lang and J. P. Chapin at Medje, Zaire, on September 8, 1910.

Distribution

Norhteastern Zaire, Uganda and Cameroun.

Specimens Examined (20)

Uganda: Budongo Forest near Masindi, 8 ♂♂, 12 ♀♀ (ROM)

Measurements

As shown in Table 35.

Comments

Koopman (1965) confirmed the specific status of this bat, which is commonly known as the Medje greater free-tailed bat. But he doubted the validity of *T. trevori*,

described by J. A. Allen (1917) from Faradje, Zaire, and considered trevori to be a subspecies of congicus. Hayman and Hill (1971) mentioned that T. S. Jones had obtained 10 specimens from the West Nile District, Uganda, that agreed closely with the description of T. trevori and supported Koopman's suggestion that T. trevori is the savanna form of the forest-living T. congica. Peterson (1972), however, demonstrated that adult male T. congica were significantly larger than adult male T. trevori in nine of 15 parameters, and that adult female T. congica were significantly larger than adult female T. trevori in 11 parameters, and therefore considered T. congica and T. trevori to be valid taxa.

T. congica has a uniform Mummy Brown colour on the dorsum and Pallid Mouse Gray on the venter. Basisphenoid pits are deep, round and large. The third commissure of the last upper molar is more reduced than in T. trevori.

TABLE 35

Sample statistics of male and female Tadarida congica.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	8	56.91	0.47	55.40-59.60	12	56.40	0.32	54.20-57.80
3MET	8	58.61	0.39	57.20-60.30	12	57.75	0.38	55.10-59.30
3M1P	8	25.72	0.41	23.30-26.90	12	25.23	0.34	22.20-26.40
3M2P	8	22.25	0.21	21.40-23.30	12	21.66	0.31	19.40-22.90
4MET	8	56.24	0.28	55.10-57.40	12	55.56	0.31	53.70-56.80
4M1P	8	21.27	0.23	20.30-22.10	12	21.12	0.27	19.00-22.10
4M2P	8	10.69	0.20	10.00-11.60	12	10.36	0.23	9.00-11.50
5MET	8	33.52	0.22	32.50-34.50	12	32.88	0.26	31.10-34.00
5M1P	8	16.02	0.21	14.90-16.90	12	15.67	0.16	14.70-16.50
5M2P	8	4.92	0.26	3.80- 5.90	12	4.81	0.09	4.20- 5.20
GSLN	8	25.91	0.17	25.30-26.60	12	25.25	0.09	24.70-25.70
CDIN	8	23.65	0.15	23.05-24.35	12	23.04	0.08	22.50-23.50
PALL	8	10.45	0.12	9.85-10.90	12	9.86	0.06	9.55-10.20
ZYGO	8	15.67	0.11	15.25-16.15	12	15.25	0.07	14.95-15.55
MAST	8	13.91	0.12	13.30-14.40	12	13.60	0.10	12.70-14.10
BBCS	8	12.47	0.10	12.00-12.95	12	12.19	0.06	11.75-12.65
HBCS	8	8.05	0.07	7.80- 8.40	12	7.84	0.05	7.40- 8.05
ROWL	8	9.19	0.09	8.90- 9.60	12	8.65	0.05	8.40- 8.90
IOWA	8	7.97	0.09	7.50- 8.30	12	7.57	0.08	7.10- 7.90
POCN	8	4.81	0.06	4.50- 4.95	12	4.76	0.03	4.60- 5.00
M3M3	8	10.74	0.08	10.45-11.10	12	10.58	0.06	10.30-10.85
CANM	8	9.33	0.06	9.10- 9.50	12	9.10	0.04	8.90- 9.40
CANC	8	7.62	0.09	7.15- 8.00	12	7.02	0.06	6.50- 7.30
CANH	8	5.26	0.07	4.90- 5.45	12	4.61	0.05	4.40- 5.05
WBSP	8	0.84	0.05	0.65- 1.10	12	0.82	0.06	0.60- 1.25
LBSP	8	1.81	0.12	1.40- 2.45	12	1.83	0.05	1.55- 2.10
CNIL	8	17.97	0.12	17.40-18.50	12	17.45	0.06	17.15-17.80
GMLN	8	18.81	0.14	18.05-19.30	12	18.15	0.08	17.65-18.65
LCAM	8	10.56	0.07	10.30-10.90	12	10.08	0.05	9.75-10.40
LCAC	8	3.66	0.05	3.40- 3.85	12	3.27	0.03	3.10- 3.45
LCAH	8	4.26	0.07	4.04- 4.50	12	3.57	0.05	3.20- 3.85

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.

See text for character abbreviations.

Tadarida (*Mops*) *trevori* (J. A. Allen)

Mops trevori J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist. 37: 468. Faradje, Zaire.

Mops niangarae J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 467. Niagnara, Zaire.

Tadarida (*Mops*) *congicus trevori* Koopman, 1965, Amer. Mus. Novitates, 2219: 29.

Tadarida (*Mops*) *niangarae* Koopman, 1965, Amer. Mus. Novitates, 2219: 29.

Tadarida (*Mops*) *trevori* Peterson, 1972, Life Sci. Contr., Roy. Ont. Mus., 85: 10.

Holotype

An adult ♀ (AMNH 49250), collected by H. Lang and J. P. Chapin at Faradje, Zaire, on September 29, 1912.

Distribution

Savanna zone in northeastern Zaire, Uganda and Sudan.

Specimens Examined (4)

Sudan: Yambio, 1 ♀ (ROM)

Uganda: Budongo Forest, near Masindi, 1 ♂ (ROM);
Metu, W. Nile District, 2 ♀♀ (ROM).

Measurements

As shown in Table 36.

Comments

T. trevori as shown above is a valid species and distinct from T. congica. The only species conspecific with T. trevori is T. niangarae. Peterson (1972) showed that T. niangarae, described by J. A. Allen (1917) from Niangara, Zaire, is a junior synonym of T. trevori. He demonstrated that the single diagnostic character that distinguishes T. niangarae, which is the absence of the connecting band between the ears of the holotype is an artifact of preparation.

T. trevori has a Cinnamon-Brown colour on the dorsum and pale brown colour in the venter with bands of dark brown laterally. The length of the third commissure of the last upper molar varies individually but is generally more pronounced than in T. congica. In a subadult specimen (LCAM 27438), it is well developed on the right side and absent on the left (Peterson, 1972).

TABLE 36

Sample statistics of male and female Tadarida trevori.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	1	53.70	--	--	3	52.53	1.11	50.40-54.10
3MET	1	54.50	--	--	3	54.73	0.45	54.10-55.60
3M1P	1	23.50	--	--	3	23.72	0.38	23.10-24.40
3M2P	1	21.80	--	--	3	22.10	0.55	21.20-23.10
4MET	1	51.90	--	--	3	52.40	0.12	52.20-52.60
4M1P	1	19.20	--	--	3	19.40	0.40	18.90-20.20
4M2P	1	12.00	--	--	3	11.60	0.21	11.20-11.90
5MEt	1	32.90	--	--	3	32.73	0.42	32.30-33.60
5M1P	1	14.40	--	--	3	15.67	0.09	15.50-15.80
5M2P	1	6.00	--	--	3	5.40	0.10	5.20- 5.50
GSLN	1	24.10	--	--	3	24.00	0.21	23.70-24.40
CDIN	1	21.70	--	--	3	21.47	0.49	20.50-22.10
PALL	1	9.20	--	--	3	9.43	0.13	9.20- 9.65
ZYGO	1	14.50	--	--	3	14.73	0.12	14.50-14.90
MAST	1	13.90	--	--	3	13.82	0.07	13.75-13.95
BBCS	1	11.80	--	--	3	12.02	0.09	11.90-12.20
HBCS	1	8.20	--	--	3	7.47	0.18	7.20- 7.80
ROWL	1	8.70	--	--	3	8.30	0.12	8.10- 8.50
IOWA	1	8.40	--	--	3	6.90	0.15	6.60- 7.10
POCN	1	4.90	--	--	3	4.97	0.07	4.90- 5.10
M3M3	1	10.30	--	--	3	10.13	0.07	10.00-10.20
CANM	1	8.90	--	--	3	8.58	0.04	8.50- 8.65
CANC	1	6.70	--	--	3	6.73	0.20	6.40- 7.10
CANH	1	4.60	--	--	3	4.32	0.13	4.10- 4.55
WBSP	1	0.65	--	--	3	0.70	0.09	0.55- 0.85
LBSP	1	2.60	--	--	3	2.40	0.06	2.30- 2.50
CNIL	1	15.40	--	--	3	16.55	0.13	16.30-16.70
GMLN	1	16.60	--	--	3	17.08	0.06	17.00-17.20
LCAM	1	9.50	--	--	3	9.53	0.09	9.40- 9.70
LCAC	1	3.50	--	--	3	3.23	0.03	3.20- 3.30
LCAH	1	3.20	--	--	3	3.08	0.02	3.05- 3.10

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.

See text for character abbreviations.

Tadarida (Mops) midas (Sundevall)

Dysopes midas Sundevall, 1943, Kgl. Svenska Vetensk. Akad. Handl, 1842: 207. Bahr el-Abiad (=White Nile), Sudan.

Mops midas J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37: 466.

Tadarida (Mops) midas Ellerman, Morrison-Scott and Hayman, 1953, Southern African Mammals: 70.

Cotype

An adult ♂ (BMNH 46.6.2.20), from Bahr el-Abiad (=White Nile) Sudan, holotype probably in Stockholm Museum.

Distribution

Open woodland and savanna from Senegal to Nigeria, Zaire, Sudan, Ethiopia, Zambia, Rhodesia, Malawi, Botswana and Malagasy.

Specimens Examined (20)

Botswana: Maun, 10 ♂♂, 10 ♀♀ (ROM).

Measurements

As shown in Table 37.

Comments

The Sundevall's free-tailed bat was reported from Madagascar (=Malagasy) as a distinct species by Grandidier

in 1869 and named T. miarensis, but tentatively regarded by Hayman and Hill (1971) a race of midas. G. M. Allen (1939) suggested that T. midas was actually Mops rupellii (Temminick, 1827), but R. W. Hayman in Ellerman and Morrison-Scott (1951: 134) stated that Allen was incorrect and that T. midas is a distinct species.

T. midas is the largest in the subgenus Mops and is only approached by T.(T.) africana and T.(T.) teniotis in the subgenus Tadarida. T. midas is distinguished from both, however, by the absence of the third commissure on the last upper molar and the closed palate.

Kock (1969b) suggested that the type locality of T. midas is Jebel el Funj between the White Nile and the Blue Nile, Sudan. Accordingly, Koopman (1975) restricted the type locality to the west bank of the White Nile in the neighbourhood of latitude 11° 45'N, longitude 35° 30'E in the Blue Nile province. But Sundevall described the type locaility as Bahr el-Abiad which is the area south of Omdurman (15° 19'N, 32° 29'E) and commonly known as Bahar Abiad. In 1977 I collected 267 T. midas from Jebel Aulia (15° 19'N, 32° 31'E) in this area and I therefore restrict the type locality to lie within this vicinity.

TABLE 37

Sample statistics of male and female Tadarida midas.

CHARACTER	MALES				FEMALES			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
FOAR	10	62.64	0.41	60.00-64.00	10	62.23	0.26	61.20-63.80
3MET	10	63.48	0.34	61.20-64.90	10	63.77	0.20	63.00-64.80
3M1P	10	27.24	0.31	25.20-28.60	10	26.93	0.25	25.10-27.80
3M2P	10	26.63	0.44	24.30-28.70	10	26.28	0.25	25.00-27.50
4MET	10	61.28	0.26	59.20-62.00	10	61.76	0.32	60.00-63.30
4M1P	10	21.91	0.26	21.00-22.90	10	21.68	0.24	20.50-23.00
4M2P	10	16.40	0.31	14.50-17.30	10	16.19	0.21	15.10-17.20
5MET	10	37.96	0.33	36.80-40.00	10	37.90	0.24	36.80-39.10
5M1P	10	18.45	0.21	17.00-19.30	10	18.36	0.18	17.50-19.40
5M2P	10	7.30	0.17	6.00- 7.80	10	7.27	0.18	6.50- 8.40
GSLN	10	28.30	0.22	27.00-29.60	10	27.02	0.15	26.50-27.90
CDIN	10	25.48	0.14	24.50-26.00	10	24.63	0.10	24.10-25.10
PALL	10	11.39	0.09	10.90-11.70	10	10.95	0.05	10.60-11.20
ZYGO	10	17.23	0.15	16.40-17.80	10	16.76	0.13	16.10-17.20
MAST	10	14.83	0.12	14.30-15.40	10	14.51	0.09	04.00-14.90
BBCS	10	12.69	0.10	12.30-13.30	10	12.56	0.09	12.20-13.00
HBCS	10	8.61	0.11	8.00- 9.00	10	8.37	0.11	7.80- 8.90
ROWL	10	9.58	0.12	8.70-10.00	10	9.32	0.09	8.90- 9.70
IOWA	10	9.24	0.07	8.80- 9.60	10	8.92	0.07	8.60- 9.20
POCN	10	4.62	0.05	4.40- 4.90	10	4.55	0.05	4.30- 4.80
M3M3	10	12.44	0.07	11.90-12.60	10	12.15	0.10	11.70-12.60
CANM	10	10.57	0.10	9.90-11.00	10	10.21	0.07	10.00-10.60
CANC	10	8.38	0.10	7.90- 8.90	10	7.72	0.08	7.40- 8.10
CANH	10	5.28	0.10	4.80- 5.70	10	4.63	0.05	4.30- 4.90
WBSP	10	1.39	0.06	1.20- 1.70	10	1.34	0.06	1.00- 1.60
LBSP	10	1.98	0.09	1.60- 2.50	10	2.11	0.04	2.00- 2.30
CNIL	10	18.70	0.14	18.00-19.20	10	18.10	0.06	17.80-18.50
GMLN	10	19.45	0.13	18.80-19.90	10	18.87	0.06	18.60-19.30
LCAM	10	11.79	0.09	11.30-12.10	10	11.41	0.04	11.20-11.50
LCAC	10	4.23	0.04	4.00- 4.40	10	3.85	0.06	3.70- 4.10
LCAH	10	4.70	0.10	4.30- 5.30	10	4.35	0.05	4.10- 4.60

N = sample size; $\bar{X}$ = mean; SE = standard error of the mean.
See text for character abbreviations.

Identification Key

To facilitate identification of taxa studied the following key may be used:

1. Third commissure of M^3 absent.....2
1'. Third commissure of M^3 present but reduced.....5
2. Palate with conspicuous median emargination separating the upper inner incisors by a space....3
2'. Palate closed, without conspicuous median emargination, upper incisors in contact.....4
3. Upper incisors converge apically, on the same horizontal plane as canines.....T. spurrelli.
3'. Upper incisors do not converge apically and are on the anteriormost projection of the premaxilla .....T. nanula.
4. Forearm less than 50 mm., scent gland at the base of penis.....T. demonstrator.
4'. Forearm more than 60 mm., without scent gland at the base of penis.....T. midas.
5. palate with median emargination.....6
5'. Palate closed.....8
6. Forearm less than 35 mm., basisphenoid pits oval, skull length about 15.8 - 17.5.....T. petersoni.
6'. Forearm more than 35 mm.....7
7. Dorsal hair extends onto the endopatagium; lambdoidal crest interrupted, not continuous;

basisphenoid pits long oval and tapering anteriorly..
.....T. brachyptera.

7. Dorsal hair does not extend onto the endopatagium, posterior dorsolateral surfaces nude; lambdoidal crest continuous; basisphenoid pits deep and round, not tapering anteriorly.....T. thersites.

8. Forearm less than 50 mm.....9

8'. Forearm more than 50 mm.....10

9. Forearm about 44 - 47 mm; large lambdoidal crest projecting posteriorly; anterior upper premolar sometimes absent or minute and external to toothrow.....T. condylura.

9'. Sagittal crest low; anterior upper premolar in line with toothrow; crown darker than back and shoulders.....T. niveiventer.

10. Forearm about 50.4 - 54.1 mm., skull length about 23.7 - 24.4 mm.; third commissure of M^3 reduced but pronounced.....T. trevori.

10'. Forearm about 54.2 - 59.6 mm., skull length about 24.7 - 26.6 mm.; third commissure of M^3 reduced but minute.....T. congica.

GAZETTER

Country names given below are abbreviated as follows: Benin = B; Botswana = BTS; Cameroun = C; Central Africa Republic = CAR; Ghana = GN; Ivory Coast = IVC; Kenya = K; Liberia = L; Nigeria = N; Sierra Leone = SRL; Sudan = SD; Togo = T; Uganda = U; Zaire = Z.

Locality	Latitude		Longitude	
	o	'	o	'
Accra (GN)	05	32N	00	15w
Adiopodoume(IVC)	05	20N	04	07W
Avakubi(Z)	01	19N	27	33E
Ayos(C)	03	53N	12	31E
Bamenda (C)	05	55N	10	09E
Banco(IVC)	05	25N	04	03W
Bertua(C)	04	34N	13	42E
Bibianaha(C)	06	27N	02	20W
Buea(C)	03	10N	12	20E
Calabar(N)	04	56N	08	22E
Doyum(GN)	05	54N	00	01E
Efulen(C)	02	47N	10	32E
Ehania(IVC)	05	14N	02	46W
Eseka(C)	03	35N	10	44E
Eshobi(C)	05	47N	09	23E
Ezime(T)	07	27N	00	56E
Faradje(Z)	03	45N	29	43E
Freetown(SRL)	08	30N	13	17W
Ghiriso(SN)	06	32N	02	20W
Idenau(C)	04	16N	08	56E

	o	'	o	'
Jebel Aulia(SD)	15	19N	32	31E
Jukwa(GN)	05	15N	01	21W
Kabanyolo(U)	00	30N	32	15E
Kade(GN)	06	05N	00	50W
Kampala(U)	00	19N	32	35E
Kisumu(K)	00	08S	34	47E
Kumasi(GN)	06	45N	01	35W
Kumba(C)	04	39N	09	26E
Lakota(IVC)	06	00N	05	43W
Lekelbi(GN)	06	56N	00	29E
Lolodorf(C)	03	14N	10	44E
Luluabourg(Z)	05	45S	22	25E
Mangala(SD)	06	45N	32	40E
Masindi(U)	01	41N	29	43E
Mawn(BTS)	20	00S	23	25E
M'Baiki(CAR)	3	53N	18	01E
Medje(Z)	02	25N	27	18E
Mengueme(C)	03	19N	11	30E
Murchison Falls(U)	02	17N	31	41E
Nanga Emboko(C)	4	38N	12	21E
Niangara(Z)	03	45N	27	54E
Nikki(B)	09	56N	03	18E
Ntui(C)	03	40N	11	41E
Obula(C)	03	48N	11	42E
Okola(C)	04	00N	11	33E
Omdurman(SD)	15	19N	32	29E
Panga(Z)	01	52N	26	23E

	o	'	o	'
Prestea(GN)	05	26N	02	09W
Sigor(K)	01	29N	35	26E
Tars Town(L)	06	13N	08	08E
Tiko(C)	04	02N	09	19E
Yabrasso(IVC)	07	26N	03	39W
Yambio(SD)	04	34N	28	21E

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